EFFECTS OF DIET QUALITY AND QUANTITY ON CARIBOU AND REINDEER

(*Rangifer tarandus*)

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A

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Abstract

Caribou and reindeer (*Rangifer tarandus*) encounter natural and anthropogenic disturbances across the landscape. In late winter, *Rangifer* encounter acute food shortages from disturbances such as icing events. Furthermore, as shrubs expand into the arctic tundra, the proportion of low quality browse may increase in the summer diet of *Rangifer*. This study evaluated how *Rangifer* tolerate 1) fluctuations in food quantity in late winter, and 2) changes in forage quality over the summer. *Rangifer* can compensate for food shortages by increasing intake after restriction, which would allow animals to restore body mass quickly during migration. High body fat reserves increase the tolerance of food shortages. During the summer, *Rangifer* can consume exclusively browse to meet daily energy requirements; however, low nitrogen supply and high toxin load would require the use of alternative forages to supplement nitrogen and reduce toxins.

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Chapter 1: Introduction

1.1 Importance of *Rangifer*

Caribou and reindeer (*Rangifer tarandus*) are an important resource for societies in northern latitudes (Klein 1991*a*, Finstad 2008). Wild *Rangifer* historically have been a food source for many northern cultures through hunting, and more recently through domestication of reindeer (*Rangifer tarandus tarandus*) in northern Europe and Siberia (Klein 1991*a*). Wild caribou in Canada and Alaska provide a subsistence food source for local residents, and also produce an economic boom for tourism and hunting (Rupp et al. 2006). In the early 2000s, caribou hunting produced 3.1 million Canadian dollars of revenue a year in the Northwest Territories, and 5.2 million American dollars of revenue a year in Alaska (Ashley 2000, Colt 2001). Reindeer are still herded in parts of Russia and northern Europe, whereas an introduced herd on the Seward Peninsula of Alaska has been successful (Finstad 2008). The importance of *Rangifer* to these northern societies has stimulated research into the ecology of *Rangifer* and how they respond to natural and anthropogenic changes in their environment.

1.2 Natural Disturbances to *Rangifer*

Rangifer are found from the subarctic boreal forest to the high arctic tundra. Consequently, these populations are exposed to a variety of disturbances associated with different latitudes, ecosystems and climates. Large-scale climate patterns associated with oscillations in ocean currents have been tied to fluctuations in caribou herds in Alaska, Greenland, and Svalbard Island (Aanes et al. 2002, Forchhammer et al. 2002, Joly et al. 2011). Icing events, associated with warmer arctic temperatures, have been shown to

limit available forage for reindeer and caribou (Klein 1991*b*, Miller and Gunn 2003, Hansen et al. 2011). Increasing winter snow depth can influence birth mass of calves the following spring (Adams 2005). Furthermore, increased wildfires in the boreal forest (Kasischke and Turetsky 2006) and on the tundra (Mack et al. 2011) have reduced the availability of lichens on caribou winter range, affecting the carrying capacity of those ranges (Joly et al. 2003, Rupp et al. 2006, Collins et al. 2011, Barrier and Johnson 2012). Additionally, increased ambient air temperatures are associated with increased insect harassment of *Rangifer* (Helle and Tarvainen1984, Mörschel and Klein 1997, Hagemoen and Reimers 2002, Witter et al. 2012). Changing climate patterns may also influence vegetation composition on the landscape in the boreal forest and tundra ecosystems. Shrubs have been documented moving north into once barren tundra communities (Tape et al. 2006, Forbes et al. 2010, Tremblay et al. 2012), and changes in summer temperatures and precipitation patterns have been shown to alter quality and quantity of spring and summer forage used by caribou (Lenart et al. 2002).

1.3 Anthropogenic Disturbances to *Rangifer*

Increased development of natural resources in the boreal and arctic ecosystems has influenced *Rangifer* populations through disturbance and loss of habitat (Johnson et al. 2005). Oil and gas exploration has affected caribou and reindeer populations in Alaska, Canada, and Russia (Klein 1991*b*, Cronin et al. 1998, Dyer et al. 2001, Cameron et al. 2005, Joly et al. 2006). Furthermore, caribou have been found to avoid mining operations, particularly open pit mines (Weir et al. 2007, Boulanger et al. 2012). Impacts of timber harvest in Canada have altered winter habitat used by caribou, and have

influenced caribou predator-prey relationships (Smith et al. 2000, Schaefer and Mahoney 2007, Wittmer et al. 2007). Other developments, such as hydroelectric dams, directly remove habitat and can disturb migration patterns for *Rangifer* (Mahoney and Schaefer 2002, Nellemann et al. 2003, Apps and McLellan 2006). On an increasingly disturbed landscape, caribou and reindeer must be able to find enough available forage, and have enough time to consume that forage, to meet daily and seasonal energy requirements.

1.4 *Rangifer* Requirements

Amongst natural and anthropogenic disturbances on the landscape, *Rangifer* still need to meet daily energy requirements for survival and reproduction. This energy is derived predominantly from carbohydrates in the forage *Rangifer* consume. Daily forage intake must provide enough usable energy to meet daily demands for basal metabolism, thermoregulation, and activity (Barboza et al. 2009). Additional energy intake is required for seasonal mass gains to accumulate energy reserves to meet energy demands for autumn reproduction, winter survival, and spring lactation (Barboza and Parker 2008, Barboza et al. 2009, Parker et al. 2009). The available energy in forage is influenced by both structural and chemical plant characteristics that may limit the ability of *Rangifer* to consume and digest the plant material (Chapin et al. 1986, Skarpe and Hester 2008). The availability of quality forage varies over the landscape and is influenced by seasonal variations in temperature and the availability of water and nutrients in the soil, fluctuating densities of ungulate populations, and natural or anthropogenic disturbances on the landscape (Searle and Shipley 2008).

1.5 *Rangifer* Adaptations

Rangifer have adapted to the constantly changing forage quality and quantity in the boreal forest and arctic ecosystems (Parker et al. 2005). *Rangifer* seasonally migrate to areas where plant phenology is predictable such as the calving grounds used by arctic herds in spring (Skogland 1984, Bergerud et al. 1990, Klein 1992, Russell et al. 1993). Furthermore, *Rangifer* are considered an intermediate feeder (Hofmann and Stewart 1972) that consume a wide variety of forage over the year including forbs, graminoids, shrubs, mushrooms, and lichens (Trudell and White 1981, Boertje 1984, Russell et al. 1993, Finstad 2008). Although lichens contain toxic phenolic compounds such as usnic acid, *Rangifer* have adapted to winter diets that consist primarily of lichens (Sundset et al. 2010). Lastly, similar to other arctic ruminants such as moose (*Alces alces*) and muskoxen (*Ovibos moschatus*), *Rangifer* have the ability to increase the size of the digestive tract to compensate for changes in diet composition and quality between seasons (Adamczewski et al. 1987, Pehrson et al. 1997, Clauss et al. 2010). Understanding how these adapations allow *Rangifer* to meet daily and seasonal energy demands is essential to manage habitats for these populations (Hobbs and Swift 1985, Hanley and Rogers 1989).

1.6 Captive Studies

It is difficult to analyze how forage availability and quality affect wild ungulates in a natural setting; therefore, most direct food intake studies have been completed with tame or captive animals (Hobbs et al. 1983, Shipley and Spalinger 1992, Gillingham et al. 1997, Rominger et al. 2000, Tollefson et al. 2010). Individual intake studies for caribou

and reindeer have been conducted on isolated (Ryg and Jacobsen 1982, Chan-McLeod et al. 1994, Aagnes et al. 1996; Storeheier et al. 2003*b,c*) or tethered animals (Holleman et al. 1979, Trudell and White 1981); however, by isolating these animals they may not exhibit social interactions that would influence intake of wild animals in a herd. Average group intake of a herd has been measured in holding pens (Barboza and Parker 2008); but this study could not compare individual intake with body size or body condition. Individual intakes have been measured in small herds of caribou (n = 5; Parker et al. 2005) and reindeer (n = 3, Storeheier et al. 2003*a*); however, a study that directly compares caribou to reindeer, with individual intakes in a herd setting, has not been completed.

1.7 Study Objectives

The objectives of this study were to evaluate how caribou and reindeer respond to changes in forage quantity in late winter, and changes in forage quality over the growing season. Specifically, I evaluated how caribou and reindeer responded to short-term food shortages in late winter and early spring, a time of year when icing events or snow conditions may limit wild caribou forage intake (Chapter 2). Furthermore, I evaluated if instantaneous intakes of caribou responded to changes in shrub quality over the growing season (Chapter 3). This study used unique individual feeding gates, designed for the cattle industry, to investigate food intake of caribou and reindeer in a herd setting (American Calan, Inc., Northwood, NH). Caribou and reindeer were trained to open and eat out of individual feeding gates (Mazaika et al. 1988, Parker et al. 2005), while maintaining the animals in a herd setting.

In chapter 2, I examined how caribou and reindeer responded to short-term food shortages by measuring daily food intake for 22 caribou and 5 reindeer using individual feed gates over a 5-week period. I also recorded body mass changes in all animals by weighing them at least twice a week, and before and after a restriction event. I also gathered daily activity counts on a subset of these caribou and reindeer. I compared responses of restricted caribou to those that were controls, and if the amount of initial measurable rump fat affected intakes. I compared similar sized caribou and reindeer to determine if subspecies responded differently to short-term restrictions under the same conditions. The data from this study gives an estimate of maximum intake rate for caribou and reindeer, and provide insights for how *Rangifer* may be able to endure short-term food shortages at the end of winter.

In chapter 3, I conducted feeding trials with individual caribou on feltleaf willow (*Salix alaxensis*) and resin birch (*Betula glandulosa*) over 10 weeks during the growing season. I investigated how plant characteristics, such as phenols and fiber content, affected instantaneous intake rates for caribou, because willows and birch have been increasing in tundra ecosystems and may become a greater component of caribou diets. Furthermore, I measured daily pelleted feed intake rates and weekly body mass change for each caribou to determine changes in appetite and body mass over the summer. I also looked at how temperature and day length affected daily intake, and examined the relationship between food intake and increasing rump fat over the summer. Using the data from the feeding trials, pelleted feed intake, and mass gain, I developed a model that predicted the required amount of feltleaf willow or resin birch a caribou would need to

consume to meet daily energy demands for maintenance and growth over the summer, in addition to the time required to consume that forage. The data from this study can be used to determine the carrying capacity of seasonal caribou ranges on barren tundra that have an increasing shrub component.

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Chapter 2: Responses of Caribou and Reindeer to Food Shortages in Spring[1]

2.1 Abstract

Caribou and reindeer can lose foraging opportunities during late winter and early spring on migratory routes and calving grounds due to weather and snow conditions. We measured individual food intake, body mass, and activity of two-year old unbred female caribou and reindeer from 25 April to 29 May 2011. Caribou were split into a control and treatment group whereas reindeer were studied as a treatment group. Control caribou received food *ad libitum* for the 5-week study. Treatment groups were restricted every other day, for 3 days in weeks 2 and 4 (50% average *ad libitum* in week 2, 75% average *ad libitum* in week 4), and received food *ad libitum* during the rest of the study. Caribou lost 2-3% of body mass on days when average daily dry matter (DM) intakes (63 g DM $kg^{-0.75} d^{-1}$) were restricted. Caribou regained body mass as intake increased to 98 g DM $kg^{-0.75} d^{-1}$ following restriction without a change in digestibility (82-83%). In reindeer, digestive efficiency increased (78 to 83%) as intakes decreased (67 to 45 g DM $kg^{-0.75} d^{-1}$) in spring. Although reindeer were less active than caribou, food restriction did not affect activity for either subspecies. Both caribou and reindeer have "spare capacity" to increase daily food intakes to compensate for lost foraging opportunity and to use high-quality forage emerging in spring. We predict that caribou could tolerate up to one day lost foraging time on a 60% digestible diet, typical of a late winter diet, if biomass is

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sufficient to attain a maximum intake of 98 g DM $kg^{-0.75}$ d^{-1} when energy demands are moderate (950 kJ $kg^{-0.75}$ d^{-1}). Wildlife managers, when evaluating the effects of disturbance on caribou and reindeer herds, should consider the prevailing energy demands of the herd for reproduction, thermoregulation, and avoidance activities, in relation to quality and quantity of forage in adjacent areas where the herd may relocate if disturbed.

2.2 Introduction

Movement and productivity of large herbivores are influenced by spatial and temporal variations in the availability of forage plants that may be caused by natural disturbances (e.g., wildfires, icing events) and human development (e.g., agriculture, industry, urbanization). Ruminants can compensate for these variations in food by consuming a wide range of foods (Forbes 2007), migrating to different areas (Albon and Langvatn 1992), or changing behavior and physiology (Parker et al. 2009). Caribou (*Rangifer tarandus*) have adapted to the environment of arctic and boreal forest ecosystems by consuming a wide variety of forages from lichens to sedges and woody browse (Boertje 1984, Parker et al. 2005), migrating to calving areas where plant phenology is predictable (Bergerud et al. 1990), or altering the size of the digestive tract to compensate for changes in diet (Adamczewski et al. 1987). In late winter and spring, caribou may encounter short-term food shortages due to weather and snow conditions, prior wildfires, or altered migration routes (Whitten 1996, Ferguson and Messier 2000, Lenart et al. 2002, Adams 2005, Joly et al. 2010). Furthermore, variation in patch size,

abundance of quality forage, and distance between patches can also influence intake rates (Johnson et al. 2001, Searle et al. 2005).

Intake rates for caribou fluctuate daily due to spatial variation in food abundance (e.g., different ecological sites within calving grounds; Russell et al. 1993, Griffith et al. 2002), lost foraging time associated with insect harassment (Mörschel and Klein 1997; Colman et al. 2001, 2003; Witter et al. 2012), and increased vigilance to detect predators (Bøving and Post 1997). Although animals can increase intake to compensate for lost foraging opportunities, this response is limited by gut capacity and digestibility of the forage (Kie 1999, Colman et al. 2003, Searle et al. 2005, Barboza et al. 2009). Compensatory intake may be affected by reduced efficiency because digestive efficiency may decline if increased food intake reduces the time available for digestion. The net gain of energy from digestion may also decline if increased food intake is associated with greater activity for foraging. Compensatory intakes may be further modulated by seasonal changes in temperature and photoperiod that cue changes in activity and body condition for the annual cycle of growth and reproduction (Ryg and Jacobsen 1982, Tyler et al. 1999, Barboza and Hume 2006).

Quantifying maximum intake for caribou is difficult in a field setting, and often confounded by variation in the quality of forage within a feeding patch and across the landscape (Johnstone et al. 2002, Jorgenson et al. 2002). Caribou and reindeer (*Rangifer tarandus tarandus*) generally feed in groups; however, individual intake has usually been measured on isolated (Ryg and Jacobsen 1982, Chan-McLeod et al. 1994, Aagnes et al. 1996; Storeheier et al. 2003*b,c*) or tethered animals (Holleman et al. 1979, Trudell and

White 1981). Although average group intake has been measured by holding pen (Barboza and Parker 2008), those studies cannot compare individual intake with body size or body condition. Individual intakes have been measured in small groups of caribou (Parker et al. 2005) and reindeer (Storeheier et al. 2003*a*); however, caribou and reindeer have not been compared directly under the same conditions. Direct comparisons between subspecies of *Rangifer* have found differences in body fat content and mobilization between high arctic reindeer from Svalbard (*R. t. platyrhynchus*) and those from mainland Norway (*R.t. tarandus*), which were accompanied by differences in cold sensitivity and tolerance of fasting (Nilssen et al. 1984). Two subspecies of *Rangifer* are also found in Alaska: the native Barren Ground caribou (*Rangifer tarandus granti*), and reindeer (*R. t. tarandus*), which were introduced from Siberia. In Alaska, caribou are predominantly migratory whereas reindeer are relatively sedentary and typically store more fat than caribou (Bergerud 2000, Finstad 2008, Hummel and Ray 2008).

We examined the relationship between body fat and food during spring when low food abundance often coincides with low body fat stores and animals must recover quickly from lost foraging opportunities to survive until plants emerge for the growing season. Young animals and pregnant females may be most vulnerable to interruptions in foraging because their demands for energy and nutrients are high but their stores of body fat may be relatively low. Thus, we studied caribou and reindeer in their second spring at the same location with the same diet to measure the effect of short-term food restriction on compensatory food intake, body mass and activity of animals that were entering their first year of reproduction. We hypothesized that young caribou exposed to short-term

food shortages in spring would have greater changes in weekly food intake, body mass, or activity than caribou fed *ad libitum*. Furthermore, we predicted that caribou with low body condition would have a higher response (changes in food intake, body mass, or activity) to short-term food shortages in spring than caribou in high body condition. Lastly, we predicted that caribou and reindeer with similar body condition would have the same changes in food intake, body mass, and activity in response to short-term food shortages in spring.

2.3 Study Area

All procedures for care, handling, and experimentation were approved by the Institutional Animal Care and Use Committee, University of Alaska, Fairbanks (Protocol #131442). A single cohort of female caribou and reindeer, born in 2009, was studied at the University of Alaska, Fairbanks - Robert G. White Large Animal Research Station (LARS), located in Fairbanks, Alaska, USA. Caribou calves were captured from wild caribou herds in interior Alaska (Delta, Hodzana, Macomb, Ray Mountains, and White Mountains) and hand-reared at LARS (Parker and Barboza 2012). Reindeer calves were born and maternally raised at LARS in a captive herd of Siberian reindeer that was founded from herds originally introduced into western Alaska (Barboza and Parker 2008). All caribou and reindeer were not bred the prior autumn and had no reproductive costs during this study. Caribou were held in two different pens, and reindeer in a third pen. Pens were 1.2 – 1.9 ha with 0.5 – 0.7 ha grassland (*Bromus* spp., *Equisetum* spp.) and 0.8 – 1.2 ha woodland (*Salix bebbiana, Betula papyrifera,* and *Populus tremuloides*). Ambient air

temperature and photoperiod were recorded every 10 minutes by a weather station within 200 m of the pens (HOBO, Onset Computer, Bourne, MA).

2.4 Methods

2.4.1 Individual Food Intake

We built individual feeders to provide pelleted feed using a Calan Broadbent Feeding System (Calan gate) that was customized for the average height and width of caribou and reindeer and spaced to minimize interference between animals (Fig. 2.1A; American Calan, Inc., Northwood, NH; Mazaika et al. 1988). Each Calan gate unlocked with an individual "key" worn on the collar of the animal (Fig. 2.1B), thereby ensuring that each animal could feed at only one station.

In December 2010 we placed the Calan gate feeders in the caribou and reindeer pens, at which time animals ate out of a common feed trough. We tied open the Calan gates and provided food in both the Calan gate feeders and the common feed trough. Over the course of one week, we slowly decreased the amount of food in the common trough and increased the amount of food in the individual feeders. After we observed that all animals were eating out of the Calan gate feeders, we stopped providing food in the common trough. We gradually closed the Calan gates over a two-week period to allow the animals to adjust to pushing open the gate to access their food. In March 2011, we trained 21 caribou and 5 reindeer to their individual Calan gate. We manually opened Calan gates to train animals to their specific gate. Gates were locked in the evening and each Calan gate was inspected the following morning to determine if the animal had

gained access to their food. All animals learned to open their assigned gate within 10 days.

2.4.2 Experimental Design

We measured body condition in March 2011 after immobilizing each animal with a mixture of ketamine (7.2 mg/kg body mass; 100mg/mL Ketamine HCl; Butler Animal Health, Dublin, OH) and xylazine (0.4 mg/kg body mass; 100mg/mL Xylazine HCl; Lloyd, Shenandoah, IA). Immobilized animals were placed in a sternal position on a flat floor to measure the maximum depth of subcutaneous fat at the rump using ultrasound (Tringa Linear, Esaote-Pie Medical, Stuart, FL) following the morphological points described by Gustine et al. (2007). We assigned caribou to control (n = 10) and treatment (n = 11) groups, evenly distributing animals into each group based on initial rump fat measurements (0.2 to 5.8 cm rump fat). Reindeer were assigned to one treatment group (n = 5; 5.2 ± 1.6 cm SD rump fat), and compared to a similar treatment group of high-condition caribou (n = 5; 4.6 ± 0.8 cm SD rump fat).

We studied responses of caribou and reindeer to food restrictions from 25 April to 29 May 2011 (Julian days 115 to 149), which overlaps the mean calving dates for both reindeer (18 April) and caribou (18 May; Barboza and Parker 2008) at this location. Water was provided *ad libitum* in large troughs. We fed a pelleted ration that was formulated to meet requirements for maintenance, growth and reproduction of *Rangifer* (Barboza and Parker 2006, 2008). We measured total mass (kg) of food offered and refused from the Calan gates on a daily basis for each individual (Parker et al. 2005). A subsample (70 g) of food offered and food refused was collected daily for dry matter

(DM) analysis and to determine if animals were selecting within their food. Subsamples were further analyzed for ash, nitrogen, and neutral detergent fiber (Van Soest et al. 1991, Barboza and Parker 2006).

Control animals received food *ad libitum* every day during the entire 5 weeks (Fig. 2.2A). Treatment animals received food *ad libitum* every day during weeks 1, 3, and 5. During weeks 2 and 4, we restricted food for treatment animals on Monday, Wednesday, and Friday and provided *ad libitum* feed on Tuesday, Thursday, Saturday, and Sunday (Fig. 2.2A). We used the average *ad libitum* intake of each individual in week 1 to set restrictions for weeks 2 and 4. In week 2, restricted animals were given 50% of *ad libitum* intake on 3 days, resulting in reduced weekly feeding times to 79% (5.5 days out of 7) of the unrestricted control group. In week 4, restricted animals were given 25% of *ad libitum* intake on 3 days, which resulted in weekly feeding times that were 68% (4.75 days out of 7) of the control group. We collected fecal samples from all animals each week to estimate digestibility from the concentrations of manganese in food and feces (Barboza and Parker 2006, Barboza et al. 2009). Digestible dry matter was calculated as the product of DM and digestibility.

Animals were trained to enter a chute and stand on a platform scale (± 0.1 kg; Tru-Test Model 703, San Antonio, TX) to measure body mass. Body mass was measured twice a week during control weeks, and 3 times a week during restriction weeks, including the day of and day after the last restriction day. During weeks 1 and 2, we measured individual activity of 11 caribou and 3 reindeer with an Actical Activity Monitoring Device (Respironics, Bend, OR) placed on the collar of the animal for the

duration of the study (Van Oort et al. 2004). We deployed 4 more activity monitors in week 3 for the duration of the study for a total of 18 monitors (caribou: n = 14, reindeer: n = 4). The Actical Activity Monitoring Device is an accelerometer-based counter; we used total daily activity counts for our comparisons and did not distinguish between types of activities. We analyzed the data from the activity monitors with Actical software to determine total daily activity counts for each individual.

2.4.3 Calculations and Statistics

We transformed data for ash, nitrogen, and digestibility to the arcsine square root to meet assumptions of normality for ANOVA (Zar 1999). We used a two-tailed t-test to compare concentrations of nitrogen and ash in food offered with those of the food ingested. Dry matter intake and digestible DM intake were expressed on the basis of metabolic body mass (g DM $kg^{-0.75}$ d^{-1}). We used ANOVA in the General Linear Model of STATA 12.0 (College Station, TX) to compare groups within weeks or with repeated measurements over time, using initial rump fat as a covariate. All repeated measure variables were compared with Huynh-Feldt correction for p-values, and means are reported with one standard deviation (± SD). Weekly comparisons of control and treatment group caribou were based on averages by individual of dry matter intake, digestible dry matter intake, body mass, and activity counts. We regressed initial rump fat (for caribou comparisons), average temperature, and photoperiod (environmental variables only for unrestricted weeks 1, 3, and 5) on dry matter intake, body mass and activity using linear regression. Maximum compensatory food intakes for treatment and control animals (maximum daily value for each animal achieved during the restriction

week), using initial rump fat as a covariate, were compared for week 2 and 4 with repeated measures ANOVA.

2.5 Results

Daily photoperiod increased during the study from 17 to 21 h/d between week 1 and 5 (Fig. 2.2B). Air temperatures were low during weeks 1 through 3 when daily minima were -1 ± 2 °C and daily maxima were +11 ± 3 °C (Fig. 2.2B). Weeks 4 and 5 were warm with daily minima above freezing (+9 ± 3 °C) and maxima above 25°C (+24 ± 3 °C; Fig. 2.2B). Consequently, snow cover that was present at the beginning of the study (25 April 2011) had melted by the third week. New growth of grass (Bromus spp.) and forbs (Equisetum spp.) had also emerged in all pens by the end of the study (29 May 2011).

The pelleted diet was 7.01% ash, 38.65% neutral detergent fiber (NDF), and 2.49% nitrogen on a dry matter basis. Concentrations of nitrogen and ash of the ingested diet were not significantly different from those of the food offered (nitrogen: $t_{56} = -1.35$, $P = 0.184$; ash: $t_{56} = 0.08$, $P = 0.940$), which indicated that animals did not select pellets within the ration.

2.5.1 Control vs. Treatment Caribou

Although daily food intake varied widely among individual caribou in the control group (17 – 109 g DM $kg^{-0.75}$ d^{-1}), average daily intakes were not different from week 1 to week 5 (59 ± 17 g DM $kg^{-0.75}$ d^{-1}; Fig. 2.3A; $F_{4,36} = 1.04$, $P = 0.374$; Appendix 2.2). Daily intakes of control caribou were not significantly related to ambient temperature ($F_{1,208} = 1.06$, $P = 0.304$) or photoperiod ($F_{1,208} = 0.43$, $P = 0.514$) in weeks 1, 3 or 5.

Caribou in the treatment group compensated by increasing food intake on the days after each restriction to achieve average weekly food intakes that were similar to those of the control group in both week 2 (63 g DM kg $^{-0.75}$ d $^{-1}$; $F_{1,19} = 0.02$, $P = 0.889$) and week 4 (59 g DM kg $^{-0.75}$ d $^{-1}$; $F_{1,19} = 0.03$, $P = 0.875$). Maximum daily intakes of the treatment group after restriction were greater than those of the control group for both week 2 (94 vs. 79 g DM kg $^{-0.75}$ d $^{-1}$; $F_{1,18} = 14.03$, $P = 0.002$) and week 4 (100 vs. 74 g DM kg $^{-0.75}$ d $^{-1}$; $F_{1,18} = 25.49$, $P < 0.001$). Digestive efficiency was not affected by food restriction because digestibility of dry matter was not different between control and treatment group caribou (0.83 ± 0.03 vs. 0.82 ± 0.02 g/g dry matter; $F_{1,76} = 0.32$, $P = 0.57$). Digestible intakes of dry matter were highest in week 3 for the treatment group of caribou at an average of 59 g digestible DM kg $^{-0.75}$ d $^{-1}$ with a maximum compensatory intake of 83 g digestible DM kg $^{-0.75}$ d $^{-1}$ in week 4 following restriction.

Caribou lost 2-3% of their initial body mass (control 99 ± 11.0 kg; treatment 99 ± 12.9 kg) over the study (Fig. 2.3B; $F_{4,76} = 18.59$; $P < 0.001$; Appendix 2.3). Initial rump fat depth was positively related to initial body mass of caribou (Fig. 2.4A) and inversely related to the amount of mass lost over the study (Fig. 2.4B), that is, caribou with large fat stores weighed more and lost more mass than those with small fat stores (Appendix 2.1, Appendix 2.3). Restricted caribou also lost an average of 3% body mass the day following food restriction in both week 2 and week 4; however, 1-2% body mass was regained when food intake increased on the days after restriction. Food intake was negatively related to initial rump fat depth in both control and treatment groups ($F_{1,76} =$

18.74; $P < 0.001$); however, intakes only declined by 18% (67 to 55 g DM $kg^{-0.75}$ d^{-1}) as initial rump fat depth increased from 0.2 to 5.8 cm ($Y = -2.29X + 67.79$; $r^2 = 0.08$).

Activity counts were not significantly different between control and treatment groups of caribou in any week (Fig. 2.3C; $F_{1,42} = 1.77$, $P = 0.191$; Appendix 2.4). Daily activity counts cycled within weeks, and varied from 23-36% around the average count for each week. Activity increased in both groups at the end of the study, that is, daily counts were greater in weeks 4 and 5 than at the start of the study ($F_{4,42} = 14.45$, $P < 0.001$). Initial rump fat depth was a significant covariate of activity that declined with increasing fat depth ($F_{1,42} = 37.89$, $P < 0.001$) across both groups; however, initial rump fat depth only explained 10% of the variation in total activity counts of caribou ($Y = -15370X + 363484$; $r^2 = 0.10$).

2.5.2 Caribou vs. Reindeer

At the start of the study, daily intakes of reindeer were 58 – 81 g DM $kg^{-0.75}$ d^{-1} (weekly average = 67 ± 9 g DM $kg^{-0.75}$ d^{-1}) and similar to those of treatment caribou with large fat stores (Fig. 2.5A; 60 – 72 g DM $kg^{-0.75}$ d^{-1}; weekly average = 66 ± 5 g DM $kg^{-0.75}$ d^{-1}; $F_{8,1} = 0.05$, $P = 0.837$; Appendix 2.1; Appendix 2.2). Food intakes of reindeer declined at the end of the study and were lower than those of caribou in week 5 (45 ± 7 vs. 63 ± 10 g DM $kg^{-0.75}$ d^{-1}; $F_{8,1} = 12.06$, $P = 0.008$; Appendix 2.2). Declines in daily intakes of reindeer were related to both increasing photoperiod ($F_{1,103} = 55.10$, $P < 0.001$; $Y = -0.09X + 160.68$; $r^2 = 0.35$) and ambient temperature ($F_{1,103} = 72.81$, $P < 0.001$; $Y = -1.42X + 73.37$; $r^2 = 0.41$) in weeks 1, 3 and 5 when food intakes were not restricted. Conversely, daily intakes of caribou were not significantly affected by either day length

($F_{1,103}$ = 0.30, P = 0.585) or temperature ($F_{1,103}$ = 3.44, P = 0.067) in those unrestricted weeks. Low intakes in reindeer were accompanied by a significant increase in digestive efficiency from 79 ± 2% in week 3 to 83 ± 2% in week 5 ($F_{4,16}$ = 9.10; $P < 0.001$). However, digestible intakes of dry matter still declined from 52 to 37 g kg $^{-0.75}$ d $^{-1}$ ($F_{4,16}$ = 10.67; $P < 0.001$) over the 5 weeks in reindeer when digestible intake of high condition caribou did not change (53 ± 5.9 g digestible DM kg $^{-0.75}$ d $^{-1}$; $F_{4,16}$ = 2.88; P = 0.123).

Reindeer lost 2% of body mass over the study ($F_{4,16}$ = 3.68, P = 0.034) in a similar fashion to treatment caribou with large fat stores (Fig. 2.5B; Appendix 2.3). Reindeer also lost body mass the days following restriction (3% week 2; 1% week 4) but quickly regained that mass when intake was restored (Fig. 2.5B). Daily activity counts of reindeer were consistently lower than those of treatment caribou with large fat stores over the 5 weeks (Fig. 2.5C; $F_{1,20}$ = 52.06; $P < 0.001$; Appendix 2.4). Daily activity of reindeer also was cyclic within each week and varied from 19-28% around the weekly average count.

2.6 Discussion

Our data provided mixed support for our initial hypotheses. Restricted caribou had similar weekly dry matter intake to those fed *ad libitum* during weeks of restriction. Likewise, changes in body mass and activity counts were also similar over the course of the study between restricted and control caribou, rejecting our initial hypothesis. As predicted, lean caribou had higher dry matter intake and activity than caribou with large fat stores; however caribou with higher fat stores lost proportionately more mass, opposing our initial predictions. Lastly, restricted reindeer lost similar proportions of

body mass to restricted caribou with large fat stores; however, dry matter intake and activity were lower for reindeer than caribou over the course of the study, contrary to our initial prediction.

Caribou and reindeer have reduced intakes in winter due to low appetites (Ryg and Jacobsen 1982, Tyler et al. 1999, Parker et al. 2005, Barboza and Parker 2008). Our estimates of caribou dry matter intake (63 g DM $kg^{-0.75}$ d^{-1}) were lower than estimated intakes during late winter and spring for captive female caribou (83-85 g DM $kg^{-0.75}$ d^{-1}; Parker et al. 2005, Barboza and Parker 2008) and calculated spring values for wild caribou (85 g DM $kg^{-0.75}$ d^{-1}; Boertje 1990). These lower values for food intake may be due to a lower fiber content in the pelleted feed in our study (39% NDF vs. 45% NDF; Parker et al. 2005) and the ability to determine intake for individuals in a group (Barboza and Parker 2008). Furthermore, animals in our trial had the ability to consume senescent grass buried under the snow as well as newly emerging plants. Green biomass in the grassland areas of these pens ranged from 5 to 18 g/m^2 at the end of May, which could have provided each animal with approximately 178 g DM d^{-1} that was equivalent to 8 to 12 % of the measured intake of pelleted ration during the final week if all available vegetation was consumed. This low percentage of available grass forage indicates that animals relied upon the pelleted ration throughout the study for the majority of their dry matter intake.

Caribou can tolerate a loss of 32% in weekly foraging time by increasing daily food intake by 41% (Fig. 2.3A). Restricted caribou were able to maintain a weekly average intake by increasing average intake on the days following food restriction (92 to

104 g DM $kg^{-0.75}$ d^{-1}). The ability for caribou to increase intake following restriction indicates that caribou have "spare capacity" at the end of winter to accommodate, digest and metabolize extra food (Baker and Hobbs 1987, McWilliams and Karasov 2005, Barboza and Hume 2006, Clauss et al. 2007). Mass changes of treatment animals during restriction weeks probably reflected changes in the fill of the digestive tract as animals lost mass during a restriction but regained mass after food was provided *ad libitum*. This suggestion is supported by positive correlations between rumen fill and live mass of wild caribou and reindeer in winter (Adamczewski 1987; Tyler et al. 1999). Increased gut fill accommodates larger meals but also conserves time for digestion. Consequently, dry matter digestibility was conserved in caribou even when food intakes fluctuated widely, resulting in similar digestible dry matter intakes between control and treatment caribou. Spare capacity to hold food would allow caribou to offset declines in diet quality by achieving the same digestible intake. If caribou can sustain the maximum dry matter intake of 98 g DM $kg^{-0.75}$ d^{-1}, they could use a diet that was only 53% digestible to achieve the same digestible intake as control animals (63 DM $kg^{-0.75}$ d^{-1} x 82% digestible = 52 g digestible DM $kg^{-0.75}$ d^{-1}).

The ability to increase digestible dry matter intake with spare capacity also allows caribou to rapidly restore tissues that were mobilized when food intakes were low. Average daily intakes of digestible dry matter for caribou in unrestricted weeks were equivalent to 866 – 1078 kJ $kg^{-0.75}$ d^{-1} (gross energy density 18.4 kJ g^{-1} digestible DM; Barboza and Parker 2006). These estimates are 1.2 -1.5 times the field metabolic rate of reindeer in winter (738 kJ $kg^{-0.75}$ d^{-1}; Gotaas et al. 2000) and 2.1 – 2.7 times the standard

metabolic rate for caribou (403 kJ $kg^{-0.75}$ d^{-1}; Fancy and White 1985). Caribou were able to increase digestible energy intakes to 1522 kJ $kg^{-0.75}$ d^{-1} after restrictions that were 668 kJ $kg^{-0.75}$ d^{-1} above the daily digestible energy intakes of unrestricted controls (854 kJ $kg^{-0.75}$ d^{-1}). This ability to increase digestible energy intakes could allow animals to replenish body energy stores with up to 12 g of fat each day if digestible energy is converted to net energy at an efficiency of 69% to deposit fat at 39.3 kJ/g (Barboza et al. 2009).

Large fat stores can modulate the response to food restriction in caribou by attenuating food intakes. Our study included animals over a wide range of body mass (75 – 122 kg) typical of caribou in interior Alaska (Adams and Dale 1998), with back fat depths that spanned the range observed in wild caribou (Parker 1981, Adamczewski et al. 1987, Allaye-Chan 1991, Ouellet et al. 1997, Gustine et al. 2007) and showed a similar relationship between body mass and body fat (Fig. 2.4A; Gerhart et al. 1996). The small, but significant loss of body mass in all animals over our study (Fig. 2.3B, Fig. 2.5B) was probably associated with fat loss because initial body mass correlated with initial rump fat (Fig. 2.4A) and those animals with larger fat stores lost more body mass over the 5-week period than those with small fat stores (Fig. 2.4B). Gradual loss of fat reserves is consistent with seasonal changes observed in wild *Rangifer* cued by increasing photoperiod in late winter (Mautz 1978, Adamczewski et al. 1987, Barboza and Parker 2008). Further declines in body mass in later winter and early spring may be observed when caribou or reindeer are subjected to longer food restrictions (Aagnes and Mathiesen 1994), are exposed to lower ambient temperatures resulting in increased costs of

thermoregulation (Parker et al. 2009), or experience increased costs of locomotion during migration or flight from predators (Fancy and White 1987).

Cycles of activity reflect variation in foraging and resting patterns that are influenced by individual patterns and interactions with other animals in the herd (Collins and Smith 1989, Maier and White 1998, Colman et al. 2004) and environmental variables such as ambient air temperature (Mörschel and Klein 1997). In captive studies, feeding and weighing events further influence activity. We therefore controlled this observer bias by feeding and weighing on the same schedule each week. Individual differences in body fat for caribou had a small affect on weekly activity, that is, animals with lower fat reserves spent more time feeding (feeding in the Calan gates and foraging) to meet daily energy requirements, while animals with larger fat reserves still maintained a similar activity pattern to stay with the herd, but spent less time feeding. Caribou synchronized their daily activity regardless of restriction, that is, control and treatment caribou exhibited similar levels of activity in both restricted and unrestricted weeks (Fig. 2.5C). Synchrony among caribou was probably enhanced by the location of the Calan gates on a common fence line between the caribou pens. Reindeer were held in an adjacent pen to the caribou but their Calan gates were separated by 100 m from those of caribou. Spatial separation of feeders probably reduced synchrony in feeding and activity between reindeer and caribou in this study (Fig. 2.5C). We did not find a decline in activity after restriction of reindeer similar to that reported by Nilsson et al. (2006) probably because reindeer in our study were still influenced by the behavior of caribou in adjacent pens. Large increases in both temperature and photoperiod (Fig. 2.2B) were accompanied by

increases in daily activity of caribou in the last two weeks of the study (Fig. 2.3C). Seasonal increases in activity during spring may be associated with migratory behaviors that have been observed in both captive and wild herds of caribou (Maier and White 1998). By contrast, the activity of our captive reindeer was not affected by changes in photoperiod or temperature as observed in wild reindeer (Colman et al. 2004). Furthermore, differences in activity between reindeer and caribou were not related to differences in fat stores, but may be the result of differences between subspecies in timing of the reproductive cycle and sedentary versus migratory life histories (Maier and White 1998, Barboza and Parker 2008).

2.7 Management Implications

Both reindeer and caribou can tolerate short-term food shortages from habitat disturbances (e.g., fire, icing events) and interruptions to foraging (e.g., humans, predators, insects). Caribou can increase food intake to 98 g DM $kg^{-0.75}$ d^{-1} in spring. If diets are high quality in spring (70-80% digestible; Klein 1990), animals can use maximum intakes to offset a loss of up to 37% foraging time each week (i.e., 2.6 days). Caribou are less tolerant of food shortages as the quality of food declines to 53% digestibility. For example, if an alternative foraging area provides food that is 60% digestible, typical of later winter diets (Klein 1990), caribou can only compensate for a loss of 1 day in foraging each week and still achieve a weekly intake of 361 g digestible dry matter or 950 kJ $kg^{-0.75}$ d^{-1}. The ability to tolerate food shortages will further diminish as energy expenditures increase for reproduction, thermoregulation, and additional activity to avoid insects, predators, or humans. Tolerance to food shortages can increase

with fat reserves and with increased digestibility. Sedentary reindeer and caribou herds with large fat stores in late winter may be able to tolerate disturbances to foraging time by enhancing digestibility at low intake while using their fat stores until plant emergence. Caribou with strong migratory behaviors are able to tolerate short-term disturbances to foraging if they can access areas with abundant food of adequate quality where foraging can continue with minimal disturbance. Foraging opportunities to offset disturbance may become more limiting for caribou as numbers of animals increase in an area, that is animals in large aggregations may be less tolerant to interruptions in foraging than animals in small isolated groups. Landscapes that provide a variety of vegetation patches due to heterogeneity in aspect, altitude and plant communities will provide greater opportunities for compensatory foraging by caribou along migration routes (e.g., Sawyer and Kauffman 2011) and at calving grounds, or for sedentary caribou herds. Wildlife managers, when evaluating the effects of disturbance on caribou herds, should consider the herd composition (e.g., proportions of growing and reproductive females) and the biomass and quality of the forage available in adjacent areas (Cameron et al. 2005, Johnson and St-Laurent 2011) where the herd may relocate if disturbed.

2.8 Figures

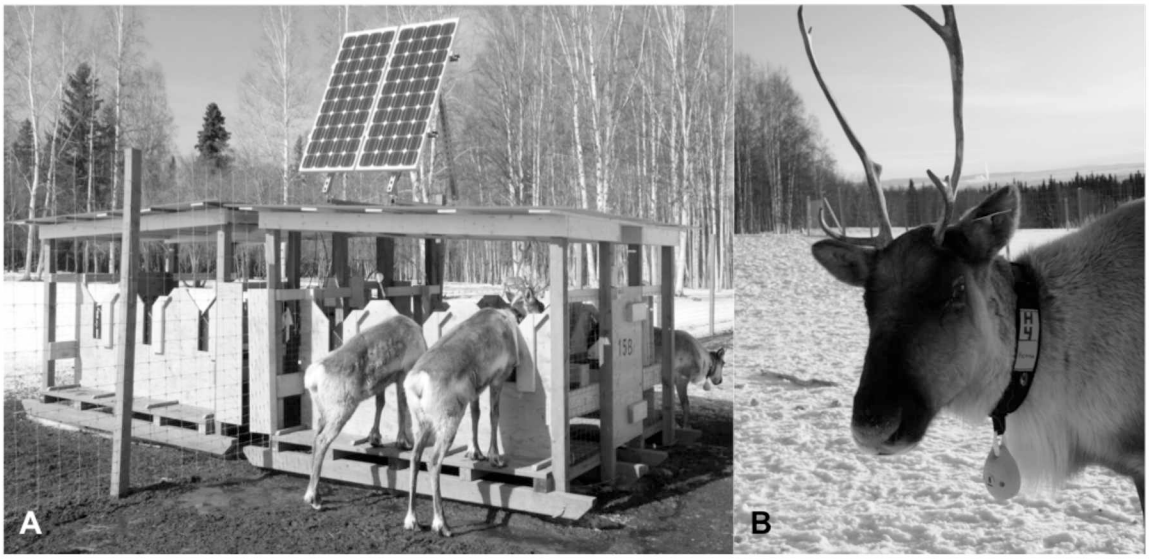

Figure 2.1. Modified Calan Broadbent Feeding System for obtaining individual food intake of caribou and reindeer at the University of Alaska, Fairbanks – Robert G. White Large Animal Research Station, Fairbanks, Alaska, USA. (A) Calan gates were built on existing feeder platforms and placed at a height to accommodate caribou and reindeer and spaced to minimize interference from adjacent animals. (B) Individual "key" attached to collar unlocked only one specific Calan gate. Photos: D. Thompson.

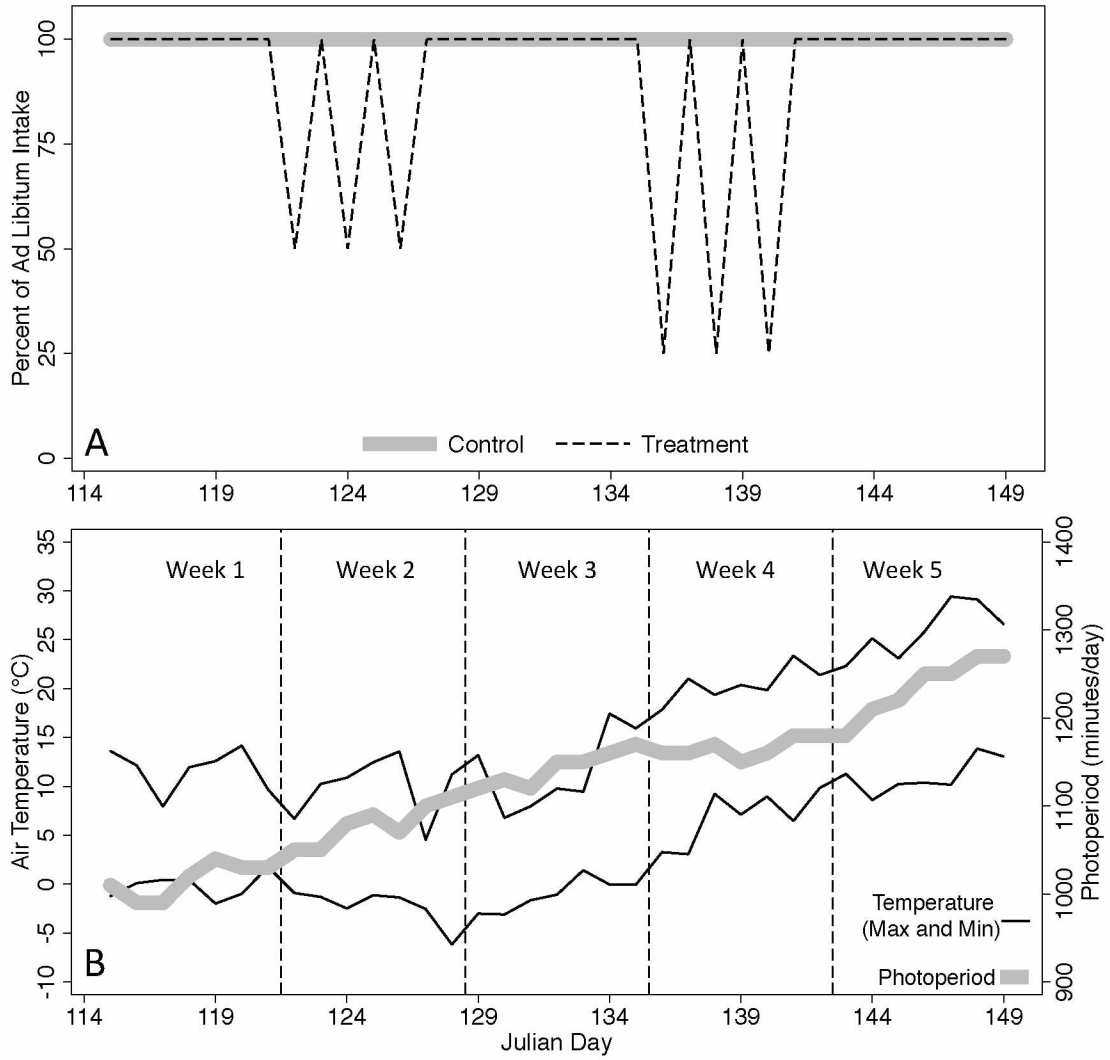

Figure 2.2. (A) Study design for control (100% *ad libitum* intake) and treatment (restricted *ad libitum* intake; 50% restriction in week 2, 75% restriction in week 4) groups and (B) experimental conditions from 25 April to 29 May 2011 (Julian days 115 to 149) at the University of Alaska, Fairbanks – Robert G. White Large Animal Research Station, Fairbanks, Alaska, USA.

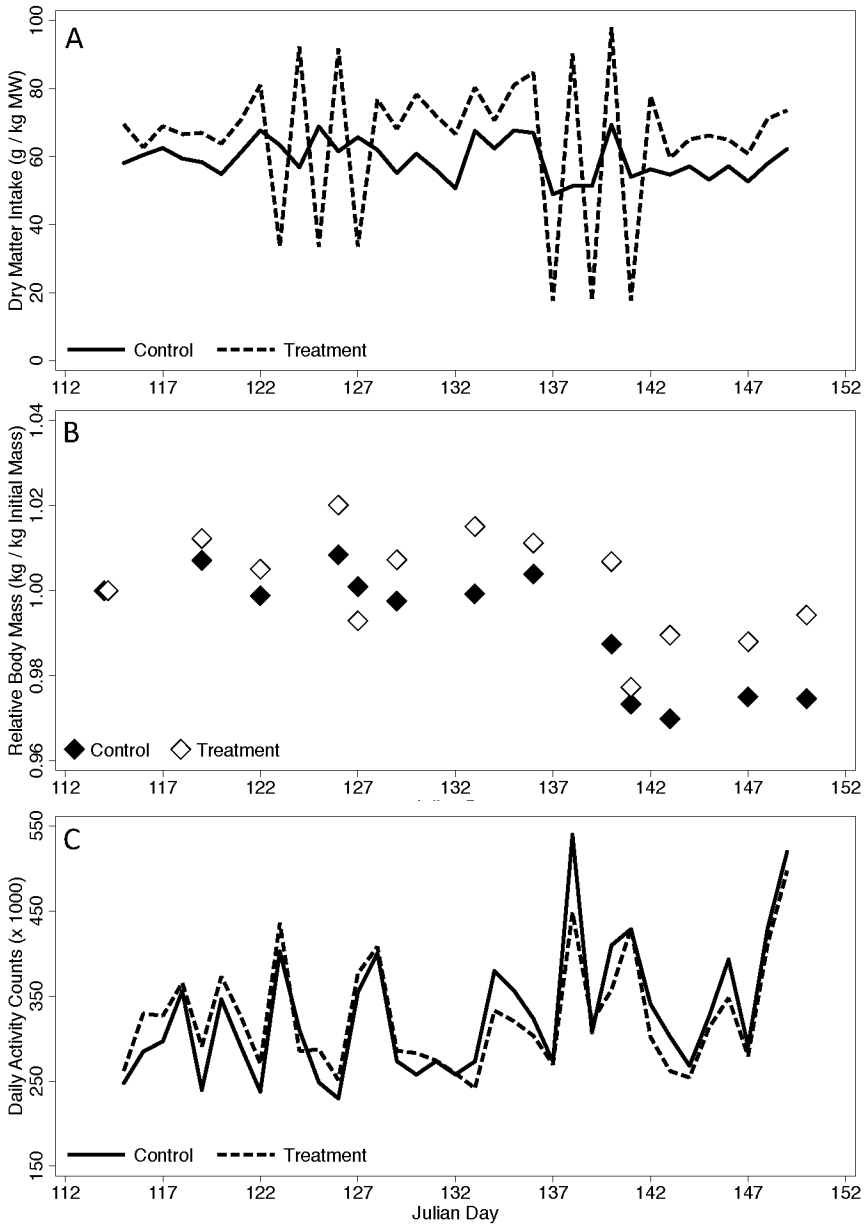

Figure 2.3. Average daily dry matter intake (A), average body mass change relative to initial body mass (B), and average daily activity counts (C) for control and treatment caribou from 25 April to 29 May 2011 (Julian days 115 to 149) at the University of Alaska, Fairbanks – Robert G. White Large Animal Research Station, Fairbanks, Alaska, USA. (MW: metabolic weight = body mass $^{0.75}$).

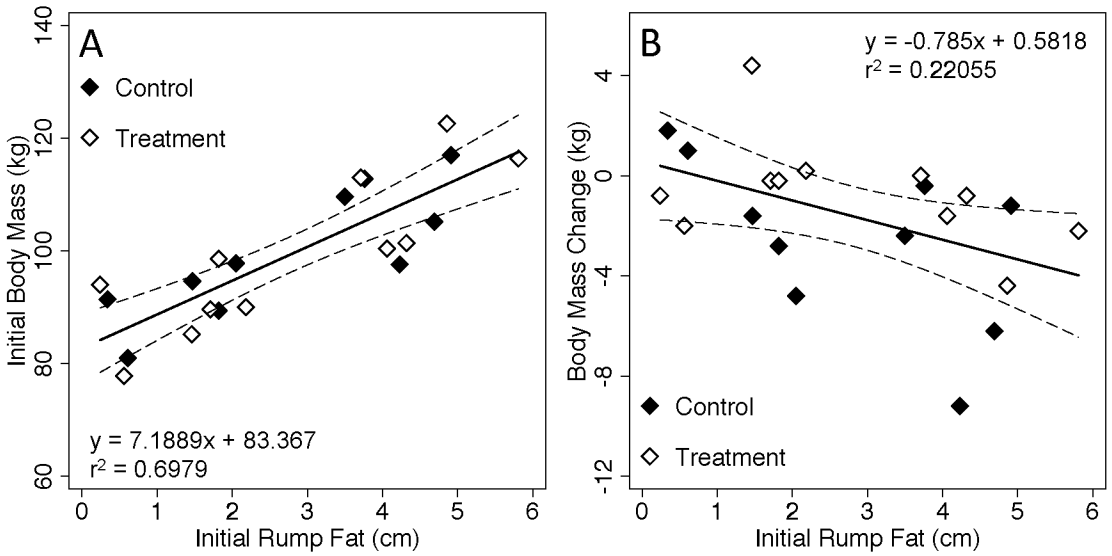

Figure 2.4. The relationship between initial body mass and initial rump fat for control (black diamond) and treatment (white diamond) caribou during week 1 (25 April to 1 May 2011) (A) and the relationship between body mass change and initial rump fat for control (black diamond) and treatment (white diamond) caribou from 25 April to 29 May 2011 (B) at the University of Alaska, Fairbanks – Robert G. White Large Animal Research Station, Fairbanks, Alaska, USA. Dashed lines are 95% confidence intervals.

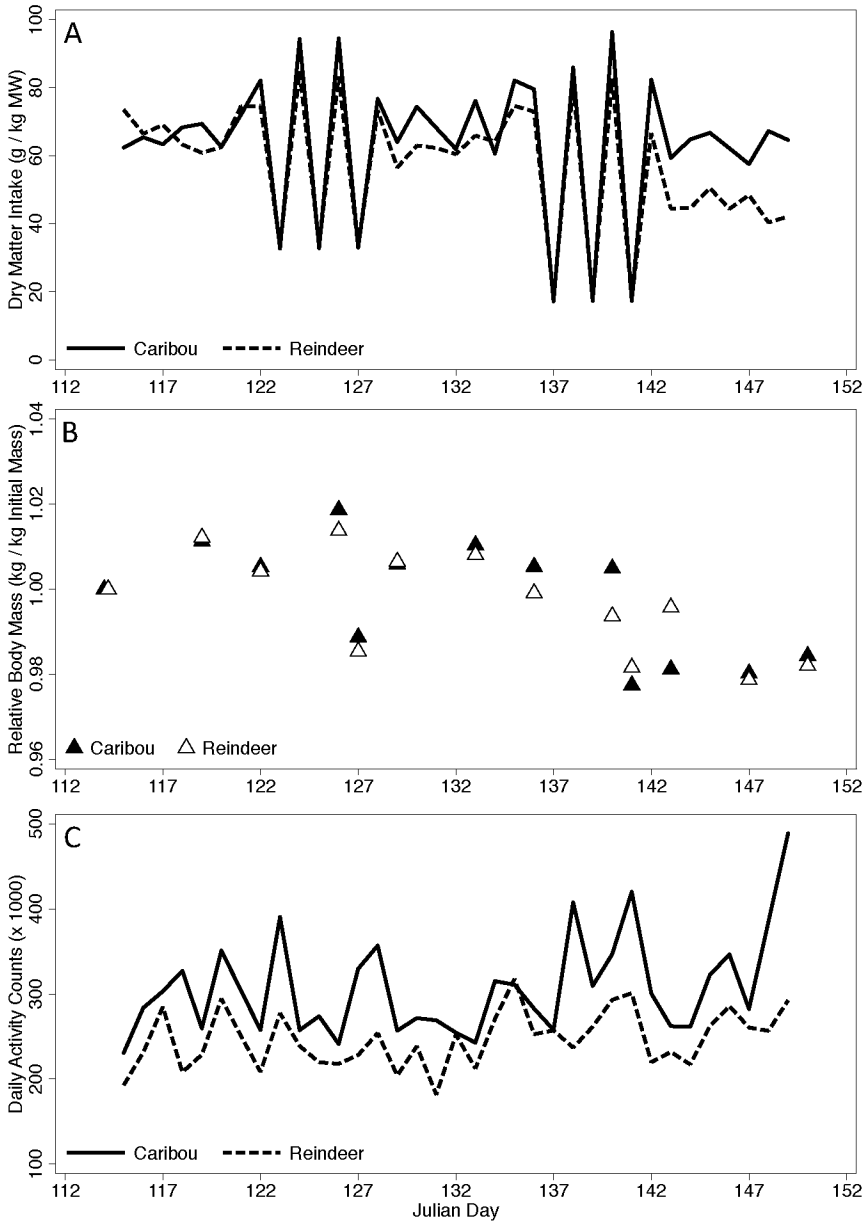

Figure 2.5. Average daily dry matter intake (A), average body mass change relative to initial body mass (B), and average daily activity counts (C) for treatment reindeer and caribou of similar body condition from 25 April to 29 May 2011 (Julian days 115 to 149) at the University of Alaska, Fairbanks – Robert G. White Large Animal Research Station, Fairbanks, Alaska, USA. (MW: metabolic weight = body mass $^{0.75}$).

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2.10 Appendices

Appendix 2.1. Maximum rump fat (cm) measured by ultrasound for caribou and reindeer at the end of March 2011, and for caribou at the end of November 2011 at the University of Alaska, Fairbanks - Robert G. White Large Animal Research Station, Alaska, USA.

Caribou			Reindeer	
	March	November		March
ID	Rump Fat	Rump Fat	ID	Rump Fat
718	4.2	5.4	927	6.91
720	3.1	3.7	928	5.09
D01	0.6	3.3	932	6.67
D02	2.0	5.8	942	3.64
D03	4.7	4.5	943	3.52
D08	0.6	2.5		
D09	0.2	5.1		
H02	4.9	6.7		
H03	5.8	NA[1]		
H04	1.5	4.7		
M02	4.9	5.9		
M04	2.2	4.3		
M05	0.3	3.0		
M06	1.5	3.3		
M08	3.5	6.7		
R01	1.8	4.9		
R02	3.8	NA[1]		
R03	4.3	7.1		
R05	4.1	4.8		
W01	3.7	6.7		
W02	1.7	4.0		
W03	1.8	NA[1]		

[1] Injured during rut and not available for November ultrasound measurement

Appendix 2.2. Daily individual dry matter intake (g / kg body mass $^{0.75}$) for caribou and reindeer from 25 April to 29 May 2011 (JD- Julian days 115-149) at the University of Alaska, Fairbanks -Robert G. White Large Animal Research Station, Alaska, USA.

	Animal ID								
	Caribou								
JD	D03[C]	R02[C]	M08[C]	718[C]	H02[C]	D01[C]	M05[C]	R01[C]	M06[C]
115	29.60	48.65	72.29	82.91	62.35	40.89	73.70	52.70	60.95
116	45.58	62.04	77.31	68.87	54.36	45.04	62.75	44.36	71.96
117	60.69	72.87	41.43	69.75	60.39	52.97	79.85	59.46	64.81
118	47.23	64.62	67.21	68.28	59.13	51.32	42.59	45.30	74.05
119	51.62	65.13	64.82	63.60	61.39	58.26	45.03	49.39	58.85
120	36.79	77.50	65.09	42.83	56.37	55.94	46.87	48.13	52.63
121	44.48	63.07	79.17	34.93	71.44	51.65	67.68	67.64	54.41
122	68.87	85.06	66.46	38.32	77.58	75.17	90.82	74.76	69.48
123	52.79	70.05	53.43	52.68	32.83	60.31	83.58	67.77	71.08
124	54.18	62.07	48.16	50.32	32.07	50.13	70.48	78.65	65.19
125	48.78	86.08	68.72	66.81	43.68	64.95	74.14	76.09	77.26
126	44.34	66.53	68.98	49.73	46.96	62.00	68.65	72.89	67.55
127	64.33	75.27	75.84	46.20	54.80	58.71	84.49	73.53	51.36
128	78.49	61.79	76.89	51.82	54.58	62.83	90.73	48.66	44.26
129	51.47	68.06	66.46	49.16	46.99	59.84	78.46	49.26	50.76
130	41.25	69.62	67.80	58.44	47.24	63.50	84.16	52.17	67.30
131	52.32	64.41	57.08	49.46	26.49	62.83	74.81	51.20	72.11
132	44.94	69.62	42.87	30.90	26.23	75.16	73.91	58.63	33.63
133	78.72	73.54	88.71	35.42	60.11	78.16	85.97	77.03	81.42
134	70.48	71.71	75.31	38.72	52.67	74.16	94.41	73.48	51.67
135	68.87	85.06	66.46	38.32	77.58	75.17	90.82	74.76	69.48
136	66.96	60.15	75.50	46.60	67.63	83.77	109.44	76.27	65.41
137	20.51	43.29	58.51	35.86	53.33	52.07	79.04	51.37	66.57
138	36.87	55.61	68.55	29.73	56.71	50.05	68.19	58.56	56.79
139	36.29	54.56	69.91	34.02	44.48	38.26	96.71	48.43	57.71
140	75.90	76.06	76.96	26.97	63.22	83.03	105.75	63.14	76.96
141	57.25	64.52	50.10	19.01	56.45	59.80	85.57	56.27	46.40
142	46.91	59.54	59.60	20.85	68.16	60.14	81.65	64.12	52.82
143	41.65	64.03	65.75	23.82	54.50	70.30	80.80	48.11	44.99
144	41.87	65.05	58.24	23.05	63.61	71.34	87.83	59.26	57.42
145	45.05	65.32	58.24	22.11	68.32	70.31	76.26	25.41	61.14
146	58.37	62.37	56.01	23.67	50.00	68.61	83.26	53.40	59.90
147	50.28	65.58	62.17	21.17	42.41	58.39	79.00	57.30	49.85
148	69.39	53.81	46.81	31.80	53.66	69.29	91.48	74.55	48.00
149	53.47	54.35	66.64	29.92	63.35	80.88	94.53	83.34	57.90

[C] Control Animal; [R] Restriction Animal; [S] Caribou compared to Reindeer

Appendix 2.2. Continued

	Animal ID								
	Caribou								
JD	D02[C]	R05[R,S]	W01[R,S]	H03[R,S]	M02[R,S]	R03[R,S]	W02[R]	W03[R]	D09[R]
115	56.86	57.01	46.98	68.50	64.91	74.36	88.83	80.05	70.21
116	72.76	64.81	40.55	69.30	76.79	75.61	82.30	77.22	56.38
117	62.96	52.55	55.85	64.01	67.26	77.01	89.06	86.66	71.08
118	74.49	59.39	73.50	75.60	65.31	67.80	85.37	78.08	58.18
119	65.55	60.81	76.36	77.11	62.87	69.67	82.30	80.71	71.68
120	66.71	55.40	64.42	65.80	62.87	64.37	71.55	72.42	67.48
121	77.37	66.80	75.32	69.83	70.93	77.21	87.22	98.72	63.58
122	30.56	76.95	83.34	79.70	75.84	94.67	96.66	85.69	84.18
123	89.45	28.15	30.41	35.26	34.00	35.64	42.90	39.74	32.36
124	57.35	86.55	103.51	92.59	85.70	103.39	109.17	89.11	98.26
125	82.13	28.15	30.41	35.26	34.50	35.64	42.90	39.74	32.36
126	67.83	90.22	103.39	97.98	79.07	101.78	107.78	91.68	89.78
127	72.21	28.15	30.41	35.26	35.48	35.64	42.90	39.74	32.36
128	50.11	63.61	86.20	77.28	70.74	85.68	79.21	82.09	80.65
129	31.26	59.68	78.16	57.07	57.71	67.40	81.66	78.15	63.66
130	56.80	66.56	78.16	59.88	75.47	91.95	83.20	91.94	67.88
131	50.57	74.58	81.80	57.07	60.96	66.29	91.25	91.07	60.94
132	50.57	47.07	81.28	50.69	69.71	60.99	88.77	82.17	66.67
133	16.51	76.30	85.82	81.08	82.20	54.98	89.39	80.74	77.22
134	21.26	60.54	82.18	65.50	64.19	30.71	87.54	69.54	74.20
135	30.56	76.95	83.34	79.70	75.84	94.67	96.66	85.69	84.18
136	17.77	73.29	92.80	76.92	78.08	76.51	92.02	92.29	84.89
137	28.53	14.27	15.28	17.90	18.82	19.69	21.53	20.00	17.67
138	32.66	80.28	95.96	87.59	79.00	86.80	98.67	81.84	91.43
139	33.58	14.27	15.28	17.90	19.33	19.69	21.53	20.00	17.67
140	45.47	90.39	109.62	93.74	88.65	99.26	104.26	99.96	106.34
141	45.16	14.27	15.28	17.90	19.33	19.69	21.53	20.00	17.67
142	48.82	79.99	93.60	73.76	81.54	82.84	59.84	77.82	93.86
143	53.02	55.01	72.09	57.18	61.26	51.21	52.87	64.94	63.54
144	43.77	62.41	79.81	56.98	59.41	65.46	68.80	63.91	65.77
145	40.08	60.07	98.38	54.87	63.55	56.80	73.84	60.40	64.55
146	56.08	56.26	70.00	62.79	64.06	57.67	68.17	70.61	71.88
147	40.69	48.35	67.31	57.50	58.30	56.22	72.58	59.34	64.55
148	40.69	64.46	88.26	59.08	66.06	58.24	77.62	65.17	77.38
149	38.23	58.31	86.67	58.29	59.59	60.26	84.24	71.01	91.43

[C] Control Animal; [R] Restriction Animal; [S] Caribou compared to Reindeer

Appendix 2.2. Continued

	Animal ID							
	Caribou			Reindeer				
JD	H04[R]	M04[R]	D08[R]	927[R]	928[R]	932[R]	942[R]	943[R]
115	83.55	64.26	65.76	70.74	76.20	78.60	57.82	84.03
116	58.45	44.94	43.22	64.54	66.11	61.06	57.92	82.69
117	77.49	62.97	54.62	63.78	68.35	70.20	67.08	75.76
118	53.70	51.66	63.61	63.02	52.65	58.37	61.85	80.47
119	15.31	67.92	72.25	61.75	42.84	60.25	60.01	79.36
120	57.18	54.78	65.34	60.74	44.25	63.48	66.04	78.26
121	53.69	54.47	60.50	74.42	52.37	79.07	79.13	87.67
122	86.15	63.53	64.61	75.24	51.62	78.20	78.03	90.10
123	31.53	27.29	30.93	32.78	31.14	32.07	31.08	40.32
124	91.14	88.01	68.92	80.64	56.45	90.24	92.93	103.75
125	31.53	27.29	30.24	32.78	31.14	32.07	31.08	40.87
126	91.14	82.87	73.30	78.85	67.22	92.65	81.84	95.89
127	31.53	27.29	30.93	32.78	30.57	32.07	31.08	39.50
128	83.55	72.52	63.75	74.12	55.70	87.20	80.39	68.80
129	86.65	63.71	55.77	50.00	42.97	67.32	60.22	62.00
130	85.07	80.82	80.26	55.43	51.99	71.35	61.54	74.49
131	83.18	62.18	63.23	59.30	46.75	70.01	65.25	70.05
132	86.96	56.98	41.85	57.49	40.94	76.45	62.60	64.77
133	103.34	88.46	64.21	69.90	58.96	61.96	70.27	68.38
134	90.43	82.96	69.54	61.11	51.11	74.57	62.30	71.64
135	86.15	63.53	64.61	75.24	51.62	78.20	78.03	90.10
136	98.12	89.81	77.04	68.84	61.97	75.58	77.76	80.55
137	15.73	15.38	17.51	17.94	16.60	16.19	15.77	22.34
138	92.71	104.06	94.93	78.90	68.46	90.33	85.89	80.67
139	15.73	15.38	17.51	17.94	17.18	15.65	15.77	22.34
140	71.54	112.73	101.38	78.38	69.33	89.24	96.42	79.55
141	15.73	15.38	17.51	17.94	17.18	16.19	15.77	21.78
142	59.85	79.27	75.22	66.15	61.50	54.09	81.67	69.45
143	58.63	57.54	61.19	50.17	35.04	33.78	52.47	50.90
144	48.33	69.86	74.74	43.27	39.57	23.61	59.34	57.02
145	65.32	65.13	65.35	43.00	49.63	36.06	59.60	63.90
146	73.97	65.45	53.43	35.88	41.34	38.00	56.95	49.56
147	56.34	68.50	60.30	40.37	49.04	49.77	54.47	48.51
148	94.05	74.49	57.77	41.42	47.56	40.37	48.90	23.54
149	93.08	86.16	60.30	43.80	44.30	36.22	51.82	34.44

[C] Control Animal; [R] Restriction Animal; [S] Caribou compared to Reindeer

Appendix 2.3. Individual body mass (kg) for caribou and reindeer from 25 April to 29 May 2011 (JD - Julian days 115-149) at the University of Alaska, Fairbanks - Robert G. White Large Animal Research Station, Alaska, USA.

	Animal ID								
	Caribou								
JD	D03[C]	R02[C]	M08[C]	718[C]	H02[C]	D01[C]	M05[C]	R01[C]	M06[C]
114	105.2	112.8	109.6	97.6	117	81	91.4	89.4	94.6
119	104.6	113.2	110.6	97.4	117.6	83.2	92.2	89	97
122	106	113.2	109.4	95.4	118.2	82.8	90.8	87	95.2
126	106.2	115.2	109.4	95.8	118.4	83.2	91.2	89	97.4
127	106	113.2	110.8	96.2	116.2	82.4	91.4	88.4	95
129	103.2	113.8	109.4	96.4	116.6	81.8	93.2	86.8	96.2
133	105.4	114.8	110.2	94.6	116.6	80.6	93	88.4	94.4
136	104	115	110.4	93.8	118	82.2	96.2	88.2	95.4
140	103.8	113.2	109	91.2	116.8	81.2	93.4	87.6	94
141	100.2	111.4	108	91	114	81.2	92.8	85.6	93.4
143	99.8	111.6	107.6	91	113.8	80.2	94	84.2	93
147	100.6	113	107.2	88	114.6	81	95.2	85	93.6
150	99	112.4	107.2	88.4	115.8	82	93.2	86.6	93

[C] Control Animal; [R] Restriction Animal; [S] Caribou compared to Reindeer

Appendix 2.3.

	Animal ID								
	Caribou								
JD	D02[C]	R05[R,S]	W01[R,S]	H03[R,S]	M02[R,S]	R03[R,S]	W02[R]	W03[R]	D09[R]
114	97.8	100.4	113	116.4	122.6	101.4	89.6	98.6	94
119	98.2	101.4	115	117.6	121	104.6	90.4	100.4	95
122	97.4	99.8	112.8	117.6	121.4	104.8	90.2	99.6	93.2
126	99	102.6	114.6	118.6	121	106.6	92.2	100.2	95.2
127	97.6	99.6	111.2	115.8	119	101.6	90	98.4	92.8
129	96.4	100.8	114	117.2	120.4	104.2	89.8	100	95.2
133	98	100.4	117	116.6	121	104.2	92	101.8	94.2
136	97	101	114.2	117.4	119.6	104	91.6	101	93.6
140	93.8	100.4	114.4	117	119.8	104.4	90.8	100.8	93.8
141	91.8	96.2	112.4	113.6	118.4	100.6	88.2	96.8	90.8
143	91	98.2	111.6	115.4	116.8	101	89.4	99.8	93
147	93	98.2	112	114	118.2	100.2	89.2	97.2	93
150	93	98.8	113	114.2	118.2	100.6	89.4	98.4	93.2

[C] Control Animal; [R] Restriction Animal; [S] Caribou compared to Reindeer

Appendix 2.3. Continued

	Animal ID							
	Caribou			Reindeer				
JD	H04[R]	M04[R]	D08[R]	927[R]	928[R]	932[R]	942[R]	943[R]
114	85.2	90	77.8	116.2	103.4	107	111.6	103.4
119	85	93.4	78.2	117.2	102.2	108	114	106.8
122	87.2	91.4	76.4	116.6	100.4	107.6	113.6	105.8
126	86.8	94.4	78	117.6	100.8	110	114.8	106
127	84.2	91.2	76.8	114.8	98.4	105.8	111	103.8
129	86.6	91.6	76.8	117	100	109.2	112.8	106.2
133	89.6	92	76.2	116.2	100	111	112.8	106
136	89.8	92.6	75.6	116	99.2	108.8	112.2	105
140	85.8	92.8	76.2	116.2	97.4	108	112.2	104.6
141	84.4	90.2	73	114.4	97	106.4	111	103
143	86.4	90.4	74.8	114.8	99.6	108.4	113.4	103.2
147	88.4	90.4	74.2	112.6	97.2	106.6	112.2	101.6
150	89.6	90.2	75.8	113.4	97.6	106.8	112	102.2

[C] Control Animal; [R] Restriction Animal; [S] Caribou compared to Reindeer

Appendix 2.4. Daily individual activity count (x 1000) for caribou and reindeer from 25 April to 29 May 2011 (JD - Julian days 115-149) at the University of Alaska, Fairbanks - Robert G. White Large Animal Research Station, Alaska, USA.

	Animal ID								
	Caribou								
JD	D03[C]	H02[C]	R02[C]	D01[C]	M06[C]	R01[C]	H03[R,S]	M02[R,S]	R03[R,S]
115	115.4	158.8	341.4	240.2		381.5	178.5		216.0
116	193.8	189.7	321.7	290.5		427.9	253.6		262.7
117	258.5	296.0	243.4	278.9		406.6	266.2		292.5
118	314.7	289.2	285.8	386.0		503.7	283.8		314.7
119	235.6	198.7	199.5	196.2		366.8	237.3		241.9
120	270.7	278.9	331.8	329.2		520.5	345.2		366.4
121	227.7	276.0	292.3	271.4		386.6	263.5		317.8
122	216.3	188.8	210.7	240.0		331.9	200.9		272.4
123	321.7	270.7	368.4	441.6		610.6	327.8		417.5
124	265.1	219.5	268.4	292.9		505.8	225.3		269.4
125	206.6	218.1	224.6	229.4		363.4	248.3		311.9
126	190.6	202.5	199.5	240.7		314.0	249.0		240.1
127	319.4	262.9	264.6	428.7		494.6	269.9		332.0
128	345.2	263.0	340.0	473.7		579.7	305.4		354.1
129	271.9	220.0	243.4	276.6		355.3	272.5		251.8
130	200.9	263.8	249.8	236.2		337.1	215.7		299.2
131	255.3	247.3	248.7	280.7		334.0	206.3		267.9
132	229.0	234.9	219.8	249.5		356.0	215.2		250.9
133	245.4	232.8	278.1	255.8	284.0	342.7	205.9		233.8
134	334.6	283.3	385.9	398.3	423.0	452.1	304.5	216.4	371.5
135	360.3	315.1	322.2	350.6	343.5	447.1	292.3	180.1	361.6
136	355.7	306.0	295.8	302.7	303.8	375.9	273.6	152.5	332.5
137	235.8	270.2	207.1	243.7	281.7	398.0	263.6	176.5	271.0
138	626.1	424.4	551.9	611.9	389.5	634.0	374.9	220.3	399.2
139	341.5	246.6	287.2	313.5	254.9	398.0	268.3	198.0	321.8
140	420.7	382.7	351.9	407.4	376.9	517.8	314.8	178.6	403.5
141	409.6	363.5	382.6	420.2	433.2	563.1	391.7	204.0	499.8
142	368.8	308.1	308.4	323.8	304.7	428.6	304.8	201.3	345.0
143	261.2	250.7	292.8	310.2	283.6	415.3	255.6	150.5	283.2
144	259.4	294.9	210.3	233.1	296.5	313.9	296.1	150.6	329.2
145	336.8	321.4	298.0	266.6	334.7	397.3	355.1	209.1	409.2
146	333.2	304.5	524.7	363.3	326.3	505.0	321.6	158.8	371.6
147	245.7	299.3	254.3	258.1	322.1	366.1	311.7	152.8	363.7
148	387.6	367.8	436.9	432.2	365.8	584.9	384.4	197.5	447.9
149	445.7	390.3	566.5	627.5	415.7	671.7	483.3	217.2	448.6

[C] Control Animal; [R] Restriction Animal; [S] Caribou compared to Reindeer

Appendix 2.4. Continued

	Animal ID								
	Caribou					Reindeer			
JD	W01[R,S]	D08[R]	D09[R]	M04[R]	W02[R]	928[R]	932[R]	942[R]	943[R]
115	298.0	190.7		356.7	333.2	232.1	212.8	133.5	
116	334.9	308.3		452.1	365.0	320.7	235.7	137.5	
117	350.7	360.4		360.1	330.0	321.2	324.1	209.5	
118	383.1	389.8		412.8	409.3	221.8	245.9	156.5	
119	299.5	325.1		333.1	306.4	247.6	281.3	156.9	
120	341.3	426.5		397.2	361.4	297.5	370.6	215.5	
121	331.2	404.5		307.0	332.4	267.0	302.5	182.6	
122	299.4	302.1		266.7	280.0	214.4	251.9	159.0	
123	426.7	454.5		510.4	479.4	290.8	336.7	204.8	
124	277.6	290.9		314.3	333.9	236.2	298.7	182.1	
125	261.2	357.8		253.3	290.9	228.3	270.8	159.7	
126	234.7	289.9		226.5	267.9	215.7	298.4	139.6	
127	387.2	411.3		410.4	449.3	243.6	270.0	171.1	
128	411.2	356.0		515.0	506.2	257.1	317.2	187.8	
129	246.4	332.9		297.0	313.8	226.3	241.7	144.4	
130	299.9	338.4		222.4	321.7	246.3	292.8	176.7	
131	332.8	310.0		246.0	282.0	173.1	238.7	133.0	
132	297.4	311.6		221.7	258.6	257.7	305.1	194.1	
133	288.5	254.4		212.8	253.6	218.3	267.5	151.6	
134	368.0	421.6	188.3	412.4	380.0	287.3	344.9	221.3	229.3
135	409.5	373.1	184.4	400.4	362.4	323.9	356.0	259.3	330.8
136	373.1	392.2	159.2	389.3	353.1	264.7	265.8	217.9	262.4
137	319.5	376.2	145.3	290.4	315.0	266.3	293.3	176.6	292.4
138	636.3	445.5	329.9	608.6	574.4	226.1	279.8	188.4	253.1
139	449.5	375.3	145.7	456.3	345.1	280.5	289.9	178.0	297.0
140	490.3	455.6	204.7	432.8	376.9	285.9	300.3	252.4	333.9
141	585.0	563.8	213.2	472.0	507.0	321.6	342.5	211.8	327.5
142	351.3	339.9	175.5	330.4	366.7	224.5	249.5	156.9	248.2
143	358.9	320.9	150.0	263.6	312.0	232.9	257.5	169.7	267.0
144	270.6	359.1	127.8	238.6	261.7	219.4	246.5	165.0	237.5
145	316.4	405.8	150.7	329.7	325.6	239.8	280.3	206.8	322.1
146	533.8	384.8	205.7	382.1	423.3	291.8	302.0	228.8	320.5
147	300.8	410.8	149.1	254.9	290.3	246.3	291.2	204.1	300.4
148	511.0	510.4	266.0	485.2	483.1	241.5	278.5	193.1	313.6
149	806.0	510.3	317.6	618.0	577.3	274.2	311.6	226.3	357.5

[C] Control Animal; [R] Restriction Animal; [S] Caribou compared to Reindeer

Chapter 3: Browse Intakes of Caribou During Summer[1]

3.1 Summary

1. Caribou (*Rangifer tarandus*) consume a mixed diet of woody browse, graminoids, lichens, and forbs in summer. We measured instantaneous intakes of two shrub species (resin birch - *Betula glandulosa*; feltleaf willow - *Salix alaxensis*) by caribou because shrubs are becoming more prevalent in the subarctic and arctic on caribou ranges. We predicted that caribou would have lower instantaneous intakes of resin birch than feltleaf willow because resin birch has smaller leaves and more phenolic toxins.
2. Resin birch and feltleaf willow changed in both form (leaf mass increased 40 - 230%) and composition (digestibility, phenols) over summer. Caribou appetite changed over the summer as daily intake of a toxin-free formulated diet increased (64.1 - 86.7 g DM $kg^{-0.75}$ d^{-1}) as animals mass also increased (96.8 - 113.5 kg). We estimated that caribou required 645 kJ $kg^{-0.75}$ d^{-1} of energy intake to maintain body mass and 1113 kJ $kg^{-0.75}$ d^{-1} to gain body mass for autumn reproduction.
3. Caribou had the same bite mass for resin birch and feltleaf willow (9.7 mg $bite^{-1}$ $kg^{-0.75}$). Caribou achieved higher bite rates for resin birch than feltleaf willow (19.4 vs. 17.7 bites min^{-1}), but instantaneous intakes were similar between forages even though resin birch contained more total phenols (64.2 vs. 32.5 %) and less

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[1] Thompson, D.P., and P.S. Barboza. 2013. Browse Intakes of Caribou During Summer: Resin Birch and Feltleaf Willow. Prepared for Functional Ecology.

available protein (6.2 vs. 10.2 %) than feltleaf willow. If animals can sustain high rates of intake, caribou would meet their daily energy demands on both forages. However, resin birch is unlikely to provide enough N to meet the demands for maintaining body protein or the additional demands for mass gain and lactation.

4. We estimated that a 100-kg female caribou would need to consume 2.4 to 8.7 kg of fresh willow or birch with a minimum eating time of 3.1 to 8.5 h day^{-1} for energy maintenance and mass gain. Variations in requirements are associated with differences in energy, moisture and digestibility of each forage. Additional energy requirements for activity or lactation will increase intake and foraging time requirements. Caribou may need to consume other forages to offset high toxin loads and low protein intakes from shrubs. Carrying capacity for caribou in an increasingly shrubby arctic may therefore depend on the abundance and diversity of plants.

3.2 Introduction

Food intakes of wild ungulates are influenced by the availability and quality of forage plants and by seasonal patterns of temperature and water availability as well as natural and anthropogenic disturbances. Interactions between these factors often reduce our ability to assess the effect of each factor on food intake in the field. For example, warmer summer conditions are expected to increase summer forage production for arctic herbivores (Turunen et al. 2009); although warmer temperatures may also increase insect harassment limiting foraging time for these same animals (Jingfors 1982, Hagemoen & Reimers 2002, Witter et al. 2012). In subarctic and arctic ecosystems, an increase in the

occurrence of shrubs, such as willow (*Salix* spp.), birch (*Betula* spp.), and alder (*Alnus* spp.), is changing the quality and quantity of forage for northern ungulates (Tape, Sturm & Racine 2006, Forbes, Fauria & Zetterberg 2010, Tremblay, Lévesque & Boudreau 2012). The leaves and stems of these woody plants contain more structural and chemical defenses against herbivores than those of forbs, grasses and sedges (Chapin, McKendrick & Johnson 1986, Skarpe & Hester 2008, McArt et al. 2009). Consequently, northern ungulates, such as caribou (Fig. 3.1; *Rangifer tarandus* Linnaeus 1758) face an increasing exposure to heavily defended forages through the summer when individuals must grow and gain mass to be able to reproduce in the autumn and/or survive the ensuing winter (Parker, Barboza & Gillingham 2009).

Caribou inhabit tundra and boreal habitats around the world, where quality and abundance of plants vary seasonally. Observational studies and fecal analysis of *Rangifer* in Alaska have indicated that 45-50% of spring and summer forage consists of deciduous shrubs, including *Betula* and *Salix* species, while the remainder of the diet predominantly consists of forbs, grasses, sedges, and lichens (Trudell & White 1981, Boertje 1984, Russell, Martell & Nixon 1993, Finstad 2008). The quality of forage available to caribou varies over the summer as plants undergo both structural and chemical changes from emergence to senescence (Chapin, Johnson & McKendrick 1980). Increasing concentrations of structural compounds (e.g., fiber) and plant secondary metabolites (e.g., tannins and phenolic residues; Kuropat 1984, Chapin et al. 1986, Finstad 2008) reduce digestible energy and protein content as the total biomass increases with vegetative growth (Johnstone, Russell & Griffith 2002). The value of habitats for

caribou can be assessed by comparing the supply of digestible energy and nutrients to those demands of the animal to estimate potential animal density or carrying capacity (number of animals per area; Hobbs & Swift 1985, Hanley & Rogers 1989) as plant communities and animal demands change with season or climate (Boertje 1985, Russell, White and Daniel 2004, Parker et al. 2009, National Research Council 2008).

We used a common garden experiment on female barren ground caribou (Fig. 3.1; *R. t. granti* J.A. Allen 1902) to measure individual daily intakes (g d^{-1}) of a formulated diet and the instantaneous intakes (g eaten min^{-1}) of two shrub species, resin birch (*Betula glandulosa* Michaux 1803) and feltleaf willow (*Salix alaxensis* Andersson 1900), that differed in leaf size and phenolic content. We predicted that caribou would have lower intakes of resin birch than feltleaf willow because resin birch has smaller leaves and higher toxin concentrations. We measured instantaneous intake throughout the summer because appetite increases as animals gain mass for winter and because plant form and composition changes over that period. We combined our measures of intake to predict daily intakes and feeding times of browse to meet demands for maintenance and mass gain of a female caribou through the summer.

3.3 Materials and Methods

3.3.1 Animals and Facilities

The Institutional Animal Care and Use Committee, University of Alaska, Fairbanks approved all procedures for care, handling, and experimentation of animals under protocol #131442. We studied adult female caribou at the University of Alaska, Fairbanks - Robert G. White Large Animal Research Station (LARS), located in

Fairbanks, Alaska, USA. Caribou were captured as calves in 2009 from wild caribou herds in interior Alaska and hand-reared at LARS (Parker & Barboza, in press). The animals used in this study were two- year-old non-reproductive females. Caribou were held in two adjacent outdoor pens (1.2 ha in size) that contained both grassland (*Bromus* spp., *Equisetum* spp.) and woodland (*Salix bebbiana* Sargent 1895, *Betula papyrifera* Marshall 1785, and *Populus tremuloides* Michaux 1803) vegetation. Ambient air temperature and day length were recorded from a weather station 3.2 km south of LARS (University of Alaska, Fairbanks, Geophysical Institute). We used 22° C as an index of over-heating for caribou because foraging time declines above that air temperature in wild caribou (Mörschel & Klein 1997).

3.3.2 Individual Measurement

Caribou were fed a pelleted ration using a Calan Broadbent Feeding System to monitor individual daily intakes for 11 weeks from 31 May to 15 August 2011 (American Calan, Inc., Northwood, NH; Mazaika, Krausman & Whiting 1988, Chapter 1). Fresh water was provided *ad libitum* at all times from a trough. The pelleted ration was based on cereal grains (15.3% corn, 22.5% barley) and roughage (20.0% alfalfa meal, 21.3% oat hulls), with protein and sugar concentrates (10.0% soybean meal, 7.5% molasses) and premixes of minerals and vitamins. This type of formulation has been used for over 12 years to meet requirements for maintenance and growth of captive reindeer (*R. t. tarandus* Linnaeus 1758) and caribou at this facility (Barboza & Parker 2006, 2008). Control animals received pelleted feed *ad libitum* for the entire study. Treatment animals were fed pelleted ration throughout the study except on the day before each feeding trial. Food

availability was restricted for the day before each feeding trial to establish a consistent appetite for measures of forage consumption (Trudell & White 1981, Shipley & Spalinger 1992). We restricted each animal to 50% of its daily average *ad libitum* intake of pelleted feed from the previous week. A subsample (70 g) of pelleted feed offered and refused was collected daily for analysis. Fecal samples were collected from all animals at the beginning and end of the study to measure digestibility of the pelleted diet against manganese as a marker (Barboza & Parker 2006, Barboza, Parker & Hume 2009). All animals were weighed weekly on a platform scale (± 0.1 kg; Tru-Test Model 703, San Antonio, TX; Chapter 1). Maximum subcutaneous rump fat was measured by ultrasound prior to this study at the end of winter in March (Chapter 1; Appendix 2.3), and following this study at the end of the breeding season in November to determine changes in rump fat over the summer (Tringa Linear, Esaote-Pie Medical, Stuart, FL; Gustine, Parker & Heard 2007).

3.3.3 Experimental Design

We studied responses of caribou to resin birch and feltleaf willow from 6 June to 12 August 2011. Twenty-two animals were assigned to one of two adjacent pens to form two herds of similar average body mass for a stable social structure within each pen through the summer. Members of each pen were assigned to one of three groups: control (Pen 1 n = 3; Pen 2 n = 3), birch trial (Pen 1 n = 4; Pen 2 n = 4), and willow trial (Pen 1 n = 4, Pen 2 n = 4). One caribou from the control group was removed in the last 3 weeks of the study due to illness. Individual feeding trials were conducted over periods of 2 weeks for a total of 5 periods (Fig. 3.2). During each two-week period, we alternated trials

between trial animals from each pen: animals from one pen one week, followed by animals from the other pen the second week. We observed 4 animals in individual feeding trials on the first day of the week for feltleaf willow and then observed another 4 animals on resin birch the following day. Within each week, feeding trials were repeated with the same animals; therefore, each animal completed 2 feeding trials during the week. In each two-week period, we completed a total of 32 feeding trials, that is, 16 trials for feltleaf willow, and 16 trials for resin birch.

Individual animals were removed from the main pens and placed in an adjacent arena during each feeding trial. Forage was fixed in a grid of holes within a wood block to hold stems upright for natural browsing (Fig. 3.1). Two observers recorded the number of bites of forage and the duration of each feeding bout. A bite was recorded each time a plant part was cropped or stripped from the plant. Feeding bouts started when the animal took the first bite from the plant, and ended when the animal had not taken a bite for 15 seconds, or switched to another activity (i.e., drinking water). Total bites and time spent feeding were recorded for 60 minutes; if an animal was still feeding at 60 minutes, the trial continued until the animal stopped feeding for two consecutive minutes. Fresh forage was used for all subsequent trials during the same day. We weighed forage (kg) before and after the feeding trial to determine biomass removed by the animal. To correct for moisture loss during the feeding trial, we collected forage samples (50 g) before and after each feeding trial. We calculated average bite rate (bites min^{-1}), average dry matter (DM) of the forage, bite mass (g DM $bite^{-1}$), and instantaneous DM intake (g DM min^{-1}) for each individual feeding trial.

3.3.4 Forage Collection

We collected feltleaf willow from a single stand adjacent to Cripple Creek (elevation 150 m) in a recently cleared power line easement (2-year old regeneration growth), approximately 3 km southwest of LARS. We collected resin birch from a single stand located in a firebreak below Murphy Dome (elevation 685 m), approximately 22 km northwest of LARS. All resin birch was less than 5 years old with little or no indication of browsing. Feltleaf willow was collected each morning before feeding trials whereas resin birch was collected the afternoon before feeding trials. Cut stems were placed in a bin of water and stored in a shed and a tent to keep the plants cool and dark until they were used for a feeding trial. We collected a representative sample of plant stems (new woody growth) and leaves that we observed the animal consume in each feeding trial to subsequently analyze forage quality (Shipley & Spalinger 1992). Additionally, we randomly collected 20 leaves of feltleaf willow and 100 leaves of resin birch to document change in leaf mass over the season. All forage samples were stored at -20° C until analyzed.

3.3.5 Chemical Analysis

Feltleaf willow and resin birch leaves were dried to a constant mass at 55 °C, then weighed to determine average leaf mass. Frozen samples of plant stems and leaves were prepared for chemical analyses by freeze drying to constant mass (Labconco Model 7755044, Kansas City, MO). Dry samples were homogenized by grinding through a Wiley mill with #20 mesh (1.25 mm). We analyzed each sample for ash, neutral detergent fiber (NDF), acid detergent fiber (ADF), and total nitrogen (N; Van Soest,

Robertson & Lewis 1991, Barboza & Parker 2006). We measured N content of ADF residue to calculate available nitrogen as total N minus ADF N. Furthermore, each sample was analyzed for total phenols (Singleton, Orthofer & Lamuela-Raventos 1999) and protein precipitation capacity of tannins (McArt et al. 2006). We converted N content to crude protein by assuming a concentration of 16 g N 100 g^{-1} crude protein (Barboza et al. 2009). Available crude protein was calculated from the difference in N content between the whole sample and the ADF residue. Digestible crude protein was calculated from total N and protein precipitation capacity (Robbins et al. 1987; McArt et al. 2009). We determined digestibility as the loss of dry matter from the sample in a two-step procedure similar to that of Tilley and Terry (1963). Milled samples of forage were weighed into 5 x10 cm polyester bags (ANKOM Technology, Macedon, NY) and first incubated for 48 h in the rumen of a fistulated reindeer. Incubation bags were removed from the reindeer, gently rinsed in tap water to remove ruminal secretions and dried to constant mass at 55 °C. Dried bags were then incubated for 6 hours in a solution of 1 N hydrochloric acid with pepsin (2 g L^{-1}) and then rinsed in water and dried again at 55° C before weighing. Gross energy content was measured at the beginning and end of the study for pelleted diet and both forages with a bomb calorimeter (Parr Instruments, Boleen, IL; Barboza & Parker 2006).

3.3.6 Calculations

Dry matter intake, for both pelleted feed and forage, and bite mass for the forage are expressed on the basis of metabolic body mass ($kg^{0.75}$). Digestible dry matter intake was calculated as the product of dry matter intake and digestibility. Digestible energy intake

was calculated as the product of digestible dry matter intake and the gross energy content of pelleted feed or forage. The digestible energy intake predicted at zero mass gain was the estimated requirement for maintenance of the body during periods 1 and 2, period 3, and periods 4 and 5. We used the average mass gain during periods 1 and 2, period 3, and periods 4 and 5 for all caribou to calculate the requirement for mass gain during the same time frames. The equivalent intake of resin birch or feltleaf willow to meet either requirement was calculated with the corresponding digestibility, gross energy content and moisture content of each forage during each period. We used instantaneous intake rate to calculate the time needed to consume the required amount of feltleaf willow or resin birch. Equivalent intakes of digestible N in forage were calculated from the available protein content. We estimated N balance on each forage by subtracting the maintenance requirement for N (0.462 g N $kg^{-0.75}$ d^{-1}; McEwan & Whitehead 1970) from the predicted intakes of digestible N.

To meet assumptions of normality for ANOVA, we transformed dietary concentrations of ash, moisture, N, and digestibility to the arcsine square root (Zar 1999). All means are reported with one standard deviation (± SD). We used ANOVA in the General Linear Model of STATA 12.0 (College Station, TX) to compare forage quality between periods and between forage species. Pairwise comparisons of forage quality between periods were adjusted by Bonferroni's method. We used principal components analysis to combine forage quality variables into two component variables that were used as covariates for comparisons of instantaneous intake. Intakes of pelleted feed were compared between control and feeding trial animals across periods using repeated

measures ANOVA with Huynh-Feldt correction for the F statistic. Body mass for the twenty-two caribou produced a bimodal distribution; we therefore used Wilcoxon signed rank test for comparisons between control and feeding trial animals. Weekly comparisons of control and feeding trial caribou were based on averages of individual dry matter intake. We used Akaike's Information Criterion (AIC) to assess the effects of week, pen, ambient air temperature, day length, and individual by regressing on dry matter intake of control caribou, selecting the model with the lowest AIC score (Quinn & Keough 2000).

3.4 Results

3.4.1 Environmental Variables

Day length increased from 1228 min day^{-1} at the beginning of the study (Julian day 151) to 1308 min day^{-1} at the summer solstice at the beginning of week 4 (Julian day 172), then declined to 994 min day^{-1} by the end of the study (Fig. 3.2; Julian day 227). Ambient air temperatures were above freezing at 15 ± 2.7° C throughout the study. Temperatures were coolest during weeks 1 and 10 when daily minima fell to 5.3° C and warmest during week 4 when daily maxima reached 30.9° C (Fig. 3.2).

3.4.2 Food Intake and Mass Gain

The nutritional quality of the pelleted ration met or exceeded that of the two forages. The pelleted ration was similar to feltleaf willow in organic matter and gross energy content (Table 3.1; $t_2 = -2.84$, $P = 0.105$). Pelleted feed was also similar in total N content to feltleaf willow ($t_{28} = 0.05$, $P = 0.959$) but contained more available N than either willow or birch because both fiber-bound N and protein precipitation capacity were low (Table

3.1). Fiber content of the pelleted feed was lower than that of either forage and thus dry matter digestibility was greater for the pelleted diet than for either willow or birch (Table 3.1).

Control animals that were not included in the feeding trials maintained low intake of pelleted feed through the first 7 weeks but maintained a high intake of food over the last 4 weeks as body mass was gained (Fig. 3.3; Appendix 3.1; Appendix 3.2). The variables week, pen, and individual best described dry matter intake for control caribou over the 11-week trial (AIC = 543.61, $F_{3,59} = 15.80$, $P < 0.001$, Appendix 3.3). Significant differences in food intake of control animals between pens ($t = -3.06$, $P = 0.003$) were probably associated with differences in rank and social structure within each pen as dominant animals displaced others around the feeding gates. For the 7 weeks centered around the solstice (weeks 1 to 7), warm temperatures above 22° C also affected dry matter intake for control caribou (Fig. 3.4A; model factors = week, pen, individual, temperature; AIC = 347.46, $F_{4,37} = 14.97$, $P < 0.001$; Appendix 3.3). During the last 4 weeks of the study, the variables week, pen, day length, and individual most influenced dry matter intake of control caribou (AIC = 182.64, $F_{4,16} = 4.00$, $P = 0.020$; Appendix 3.3). Individual differences in fattening, which were measured as changes in rump fat depth, were positively related to dry matter intake of control animals as well as those included in the feeding trials during the last 4 weeks of the study (Fig. 3.4B; $F_{1,17} = 9.83$, $P = 0.006$, $r^2 = 0.37$).

Body mass changes were similar between control and feeding trial caribou over the study as animals increased from an average of 96.8 ± 12.2 kg in week 1 to 113.5 ±

13.3 kg in week 11 (Fig. 3.3B; z = -1.637, P = 0.102). However, dry matter intake of pelleted feed was significantly different between control and feeding trial caribou (Fig. 3.3A; $F_{1,197}$ = 14.25, P < 0.001) when air temperatures were warm in week 4 (Fig. 3.2; $F_{1,19}$ = 11.06, P = 0.004) and week 6 ($F_{1,19}$ = 19.28, P < 0.001) and at the end of the mass gain in week 11 (Fig. 3.3; $F_{1,18}$ = 8.85, P = 0.008).

3.4.3 Instantaneous Forage Intake

Leaves of feltleaf willow were larger than those of resin birch throughout the season (Fig. 3.5A-B). Leaf mass of feltleaf willow was 3 to 8 times greater than resin birch on the basis of fresh mass (102-356 mg leaf^{-1} vs. 32-52 mg leaf^{-1}) and dry mass (Fig. 3.5 A-B; 76-252 mg leaf^{-1} vs. 20-30 mg leaf^{-1}; $F_{1,38}$ = 84.25, P < 0.001), even though feltleaf willow contained more moisture than resin birch (Fig. 3.5 C-D; $F_{1,38}$ = 212.06, P < 0.001; Appendix 3.4). Leaf mass of both species increased (Fig. 3.5 A-B; feltleaf willow: $F_{4,15}$ = 18.87, P < 0.001; resin birch: $F_{4,15}$ = 7.30, P = 0.002) as moisture content declined over the summer (Fig. 3.5 C-D; feltleaf willow: $F_{4,15}$ = 4.24, P = 0.017; resin birch: $F_{4,15}$ = 8.65, P < 0.001).

Individual caribou cropped new woody growth and leaves in different ways (Fig. 3.1). For feltleaf willow, caribou selected budding leaf clusters in the beginning of the study, but switched to individual leaves as the new woody growth increased in diameter and tensile strength. Although selection of individual parts was the predominant technique, caribou also stripped leaders, budding leaf clusters and mature leaves as feltleaf willow grew throughout the study. For resin birch, caribou mainly used a stripping motion to remove both new woody growth and leaves, although one individual

preferred to select individual leaves. Bite rate increased as bite mass declined for both forages (Fig. 3.6), that is, animals ate more slowly as they took larger bites or stripped leaves (resin birch: $F_{1,28} = 41.66$, $P < 0.001$; feltleaf willow: $F_{1,28} = 9.76$, $P = 0.003$; Appendix 3.5). Small leaf sizes in resin birch were associated with greater bite rates than those for feltleaf willow (Fig. 3.6; $t_{3,76} = -2.02$; $P = 0.047$). Bite mass did not differ between forages ($F_{1,56} = 1.53$, $P = 0.221$; Appendix 3.6) or within forages over the growing season (resin birch: $F_{4,28} = 1.12$, $P = 0.361$; feltleaf willow: $F_{4,28} = 1.07$, $P = 0.380$; Appendix 3.6) even though leaf size changed markedly during the summer (Fig. 3.5 A-B). However, bite rate increased over the 5 periods for feltleaf willow ($F_{4,28} = 7.06$, $P = 0.004$; Appendix 3.6) and resin birch (Fig. 3.6B; $F_{4,28} = 3.97$, $P = 0.011$; Appendix 3.6) as daily dry matter intake increased with mass gain (Fig. 3.3).

Although concentrations of mineral ash and total N were greater in feltleaf willow than resin birch throughout the summer (ash: $F_{1,38} = 345.51$, $P < 0.001$; total N: $F_{1,38} = 22.59$, $P < 0.001$), fiber components were similar between the forages (Fig. 3.7A; Table 3.1; Appendix 3.4; NDF: $F_{4,15} = 1.26$, $P = 0.328$; ADF: $F_{4,15} = 2.02$, $P = 0.143$). Gross energy content of resin birch was greater than feltleaf willow ($t_3 = 13.06$, $P = 0.001$) and consistent with the greater content of organic matter in resin birch (Table 3.1; Appendix 3.4; $F_{1,38} = 345.51$, $P < 0.001$). Concentrations of fiber (Fig. 3.7A) and N were most variable in early summer when caribou often consumed new woody growth with young leaves. Acid detergent fiber in both forages declined from mid summer as caribou selected more leaves and less new woody growth, while concentrations of phenols increased, especially in resin birch (Fig. 3.7B). Crude protein was more available and

more digestible in feltleaf willow than in resin birch ($F_{1,38} = 70.56$, $P < 0.001$) because feltleaf willow had lower protein precipitation capacity (Table 3.1; Appendix 3.4; $F_{1,38} = 54.02$, $P < 0.001$) and proportionately less N bound to fiber than did birch (Table 3.1; Appendix 3.4; $F_{1,38} = 15.60$, $P < 0.001$). Dry matter digestibility of feltleaf willow increased from mid summer to exceed that of resin birch by the end of the summer (Fig. 3.7C; Table 3.1; Appendix 3.4; $F_{1,38} = 29.27$, $P < 0.001$).

Principle components analysis of forage quality produced two components that explained 77% of the total variance in plant parts we observed caribou consuming. The first principal component (PC1) accounted for 57% of variation that was positively associated with nutrients (ash, moisture, N) and negatively associated with anti-nutrients (protein precipitation capacity and total phenols; Appendix 3.7). The second principal component (PC2) accounted for 20% of variation that was positively correlated with both ADF and NDF (Appendix 3.7). Increasing leaf mass of both forages was associated with declines in PC1 scores as nutrients declined and phenols increased with maturation of the leaf.

Instantaneous intakes were similar between feltleaf willow (0.16 ± 0.05 g DM min^{-1} $kg^{-0.75}$) and resin birch (0.17 ± 0.07 g DM min^{-1} $kg^{-0.75}$) over the 5 periods (Fig. 3.8; $F_{156} = 1.03$, $P = 0.313$; Appendix 3.5). Consistent rates of instantaneous feeding (Fig. 3.8) were not related to average daily intakes of pelleted feed that increased with mass gain of the animals (Fig. 3.3; $F_{178} = 1.06$, $P = 0.307$). Similarly, none of the measures of leaf mass, dry matter digestibility, or forage quality (PC1 and PC2) correlated with instantaneous intake rates ($P > 0.05$).

3.4.4 Predicting Daily Browse Consumption

We calculated the amount of energy and N required by a female caribou of 100 kg body mass to estimate the daily intake of willow and birch at the beginning and end of summer (periods 1-2 and periods 4-5). Digestible energy intake (kJ $kg^{-0.75}$ d^{-1}; X) for caribou on pelleted feed was positively correlated with absolute gain (g / day; Y) during the first two and the last two periods (7 June to 4 July: Y = 0.6021X -454.45, $F_{1,86} = 21.86$, $P < 0.001$, $r^2 = 0.20$; 19 July to 15 August: Y = 0.5372X -287.41, $F_{1,83} = 9.01$, $P = 0.004$, $r^2 = 0.10$) but low and variable mass changes in the middle period resulted in no correlation between digestible energy intake and absolute gain, thus we did not estimate energy and N requirements for this period (5 July to 18 July: Y = 0.3481X -238.24, $F_{1,42} = 3.29$, $P = 0.077$, $r^2 = 0.08$). Estimated energy requirements for maintenance were 755 and 534 kJ $kg^{-0.75}$ d^{-1} in periods 1-2, and periods 4-5 respectively. Estimated energy requirements for mass gain were 1090 and 1135 kJ $kg^{-0.75}$ d^{-1} in periods 1-2, and periods 4-5 respectively, which were 44 to 112% higher than those at maintenance. Predicted daily intakes of fresh forage to meet energy requirements of a 100-kg female caribou were 3.6 to 8.7 kg of feltleaf willow and 2.4 to 5.5 kg of resin birch (Fig. 3.9 A-B). Our estimates of required forage intake declined through the summer as dry matter content and digestibility increased and as the estimated maintenance requirement declined by 30% (Table 3.1, Fig. 3.5 and Fig. 3.7). The corresponding time required to consume forage each day was 3.2 to 7.4 h for feltleaf willow and 3.1 to 8.6 h for resin birch (Fig. 3.9 C-D). Nitrogen balance decreased as the forage intake at the maintenance energy requirement declined from periods 1-2 to periods 4-5. Nitrogen balances for feltleaf willow were above the

minimum required to maintain body protein but low contents of available crude protein in resin birch (Table 3.1) resulted in N balances that were only 6% above the N requirement in early summer and 29% below the N requirement at the end of the summer (Fig. 3.9 E-F).

3.5 Discussion

3.5.1 Initial Predictions

We rejected our hypothesis that caribou would have lower intakes of resin birch than feltleaf willow because resin birch has smaller leaves and more toxins. Caribou consuming resin birch had the same bite mass as caribou consuming feltleaf willow. Caribou also achieved higher bite rates for resin birch than feltleaf willow, which resulted in similar instantaneous rates of intake even though resin birch contained more phenols and less available protein. If caribou can sustain these high rates of intake, they would be able to meet their daily energy demands on both forages, but may be limited by N intake to meet the demands for maintaining body protein and increasing body mass over the summer to meet reproduction demands in the autumn.

3.5.2 Seasonal Intake and Mass Gain

In this study, body mass increased with daily intake of the formulated diet over the summer, which is consistent with other studies of *Rangifer* (Fig. 3.3; Ryg & Jacobsen 1982, Larsen, Nilsson & Blix 1985, Mesteig, Tyler & Blix 2000, Tyler et al. 1999) that reflect modulation of appetite by endogenous demands for mass gain as well as environmental factors such as air temperature (Rhind, Archer & Adam 2002). Endogenous demands for mass gain may vary with the composition of that gain over the

summer because caribou may accumulate protein stores early in the summer but deposit fat at the end of summer (Chan-McLeod, White & Holleman 1994). Our estimates of digestible energy intake for these non-lactating females at maintenance of body mass were equivalent to net energy intakes of 285 kJ $kg^{0.75}$ d^{-1} (assuming 10% gross energy loss to methane and urine, and 50% metabolizable energy loss to diet induced thermogenesis) that is similar to those estimated at 232 kJ $kg^{0.75}$ d^{-1} by Chan McLeod et al. 1994. Our data indicate that energy requirements for maintenance of body mass may change over the summer in caribou and that gains in fat stores are closely related to daily food intakes at the end of summer (Fig. 3.4B). Cool temperatures may facilitate high food intakes in late summer because the production of metabolic heat associated with feeding (diet induced thermogenesis) could cause heat stress when ambient temperatures are high (Crater & Barboza 2007; Barboza et al. 2009; Munn, Barboza & Dehn 2009). Food intake in mid summer was suppressed by high ambient air temperatures around the solstice (Fig. 3.4A), which is consistent with lower activity and feeding observed in wild caribou at temperatures above 22° C with no insect harassment (Mörschel & Klein 1997). In Norway, reindeer activity was not associated with high ambient air temperatures, although all associated observations in that study without insect harassment were below 15° C (Hagemoen & Reimers 2002). Caribou may be most sensitive to high air temperatures in mid summer when days are long and the duration of heat stress may be prolonged (Fig. 3.2); however, the relationship between duration of heat load (minutes/day above a critical temperature) and intake for caribou requires further study.

3.5.3 Forage Selection

Caribou selected a range of plant material from both feltleaf willow and resin birch over the course of the study. It was observed that caribou exerted the same amount of pressure with their lips to grasp leaves and new woody growth, and the portion that was cropped broke off at a similar tensile strength. Increasing tensile strength of forage has been found to decrease both bite size and similarly intake rate (Searle & Shipley 2008). This may also provide an inherent feedback to caribou by allowing them to select portions of the plant that have similar fiber concentrations. Our data show a slight increase, then a gradual decrease in NDF and ADF levels of ingested resin birch and feltleaf willow by caribou over the summer (Fig. 3.7A). Caribou may crop available forage on a fiber gradient associated with the tensile strength of the forage. Early in the season fiber concentrations of new woody growth would have a lower tensile strength, allowing caribou to crop the woody material and leaf buds. As the growing season progresses, fiber concentrations of the new woody growth, and associated tensile strength, increase to a point where new woody growth is no longer cropped. Our data for ash, available crude protein, digestibility, fiber, and protein precipitation capacity do not follow the traditional phenology curves found in similar arctic plants and may be a result of selection by caribou along a fiber/tensile strength gradient (Fig. 3.7; Kuropat 1984, Klein 1990, Russell et al. 1993, Johnstone et al. 2002, Finstad 2008). However, by selecting on a fiber gradient, caribou did not select against phenols, which increased over the growing season (Fig. 3.7). This implies that, at the feeding bout level, caribou foraging on resin birch or feltleaf willow may not be able to avoid ingesting large amounts of plant secondary

metabolites which are concentrated in the leaves and new woody growth of shrubs. Caribou may need to alternate to other forages that have significantly less plant secondary metabolites than these browse species while maintaining similar rates of intake to meet daily energy requirements.

3.5.4 Bite Rate

Bite rates from our study are similar to direct observation of bites in summer and autumn for woodland caribou (*R. t. caribou* Gmelin 1788; Shipley & Spalinger 1992, Rominger et al. 2000). However, these measures of bite rate (Fig. 3.6) are lower than those derived from distance observation of wild caribou or from devices measuring jaw movement of tethered reindeer in the field (65 to 186 bites/min; Trudell & White 1981, Kuropat 1984). Over the course of 160 hours of direct observation of caribou foraging, we noted that caribou take several false bites (i.e., bites without removing forage) prior to cropping vegetation, and this may explain the significantly lower bite rate in our study. Furthermore, even though resin birch had considerably smaller leaves, caribou in our study achieved a slightly higher bite rate compared to feltleaf willow. The capacity to maintain or exceed bite rates on different structural forage species allows caribou to alternate between forages while maintaining similar intake rates. By alternating forages, caribou may regulate the amount and kind of plant secondary metabolites ingested, reducing the effect of a single toxin (Estell 2010).

3.5.5 Plant Secondary Metabolites

Available energy may decrease for caribou that consume foods with plant secondary metabolites. In our study, the amount of phenols ingested increased over the summer to

meet daily energy intake requirements. At the end of summer, daily ingestion of phenols from resin birch was 183% that of feltleaf willow (Fig. 3.7B). Studies on domestic sheep indicate that phenols can suppress food intake, decreasing digestible energy intake and also reduce energy retention by increasing the loss of energy in urine as conjugated phenols (Iason & Murray 1996). Both forages in our study also contained tannins, again with levels in resin birch considerably higher than those of feltleaf willow (Table 3.1). Tannins can decrease digestibility and lower available N by binding to proteins (Robbins et al. 1987, Foley, Iason and McArthur 1999), thereby reducing protein availability by up to 46% in *Betula* and *Salix* species in interior Alaska (McArt et al. 2009). Other northern ungulates, such as moose (*Alces alces* Linnaeus 1758), produce tannin-binding salivary proteins to alleviate the effects of tannins on digestion (Hagerman & Robbins 1993), but the presence of these proteins in caribou is unknown. Our results suggest that on short-term feeding bouts, the increase of plant secondary metabolites, particularly phenols (Fig. 3.7B), did not influence instantaneous intake rates of feltleaf willow or resin birch (Fig. 3.8). Given that the animals in our study had a balanced pelleted diet and at least 2 days between feeding trials, the total load of phenols or tannins was much lower than what an animal would encounter on a diet comprised of only browse. In reindeer, it was found that rumen microbes were able to degrade the phenolic secondary compound usnic acid from lichens, but how reindeer tolerate other phenolic compounds in resin birch and feltleaf willow is not known (Sundset et al. 2010). Further intake studies on caribou are needed to quantify long-term responses to plant secondary metabolites from summer forages.

3.5.6 Intake Rate

The product of our estimated instantaneous intake rates (0.16 – 0.17 g DM min^{-1} $kg^{-0.75}$) and daily activity budgets for feeding by wild caribou (33-60%, Boertje 1985, Russell et al. 1993) gives a range of daily forage intakes from 76 to 147 g DM $kg^{-0.75}$, which encompass our measures of daily intakes of the pelleted diet for these same animals (69 - 84 g $kg^{-0.75}$) and previous estimates for lactating reindeer and caribou (124 g $kg^{-0.75}$; Barboza & Parker 2008). Over the summer, caribou can satisfy daily energy requirements from resin birch or feltleaf willow with adequate eating time at similar intake rates to other studies (Fig. 3.8 and Fig. 3.9; White & Trudell 1980, Trudell & White 1981, Shipley & Spalinger 1992). However, these estimates are based on instantaneous rates of intake, and do not account for time spent searching for food within a patch, or time spent traveling between patches (Searle, Hobbs & Shipley 2005). Furthermore, foraging time will decrease with increased vigilance for predator detection or insect harassment (Bøving & Post 1997, Mörschel & Klein 1997). High daily temperatures, together with diet-induced thermogenesis, may suppress food intake (Fig. 3.4), while small changes in forage quality can have a multiplier effect, increasing daily forage requirements (White 1983). If caribou can tolerate plant secondary metabolites in feltleaf willow and resin birch, and if they have enough time to forage to meet daily intake requirements for energy, they still may be limited by available N in both of these forages (Fig. 3.9C). Caribou may be able to sustain high intakes of feltleaf willow and resin birch, but may need alternate forage that will supplement N in the diet and limit the amount of toxins ingested from shrubs (Estell 2010).

3.5.7 Implications

Our estimates can be used to assess the value of habitats to support herds of caribou. For example, if the usable biomass of browse is 200 kg ha^{-1}, each hectare would support 20 female caribou (average body mass of 100 kg) for 7 to 8 days at maintenance or for 4 to 5 days of mass gain. These estimates are based on intakes of our captive animals, where mass gains were sufficient to result in 80% pregnancy and calving. Shrub expansion may decrease plant diversity on summer ranges for caribou and limit their ability to replenish protein and fat stores for reproduction and winter survival. Increased animal density may limit selective foraging options in areas of high concentration especially during late summer when appetites are high. Furthermore, predator or insect harassment may force caribou to temporarily relocate to less productive range that may not provide a mixed diet. Without a mixed diet, the long-term effects of plant phenols and tannins may decrease daily energy and N intakes. Further research is needed to understand the tolerance of caribou to plant secondary metabolites when food selection becomes limited and when food intakes are elevated to meet high demands for mass gain.

3.6 Figures

Figure 3.1. Caribou feeding trial on feltleaf willow (*Salix alaxensis*) at the University of Alaska, Fairbanks – Robert G. White Large Animal Research Station, Fairbanks, Alaska, USA. Photo: D. Thompson.

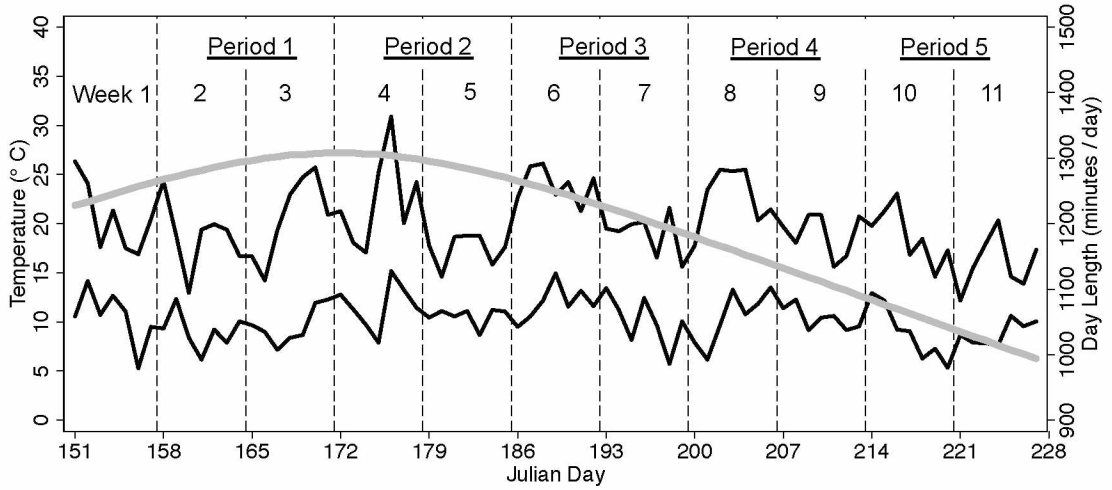

Figure 3.2. Study design (time frames) and experimental conditions from 31 May to 15 August 2011 (Julian days 151 to 227). Maximum and minimum ambient air temperature (solid lines) and day length (sunrise to sunset; gray line) recorded at the University of Alaska, Fairbanks – Geophysical Institute, Fairbanks, Alaska, USA.

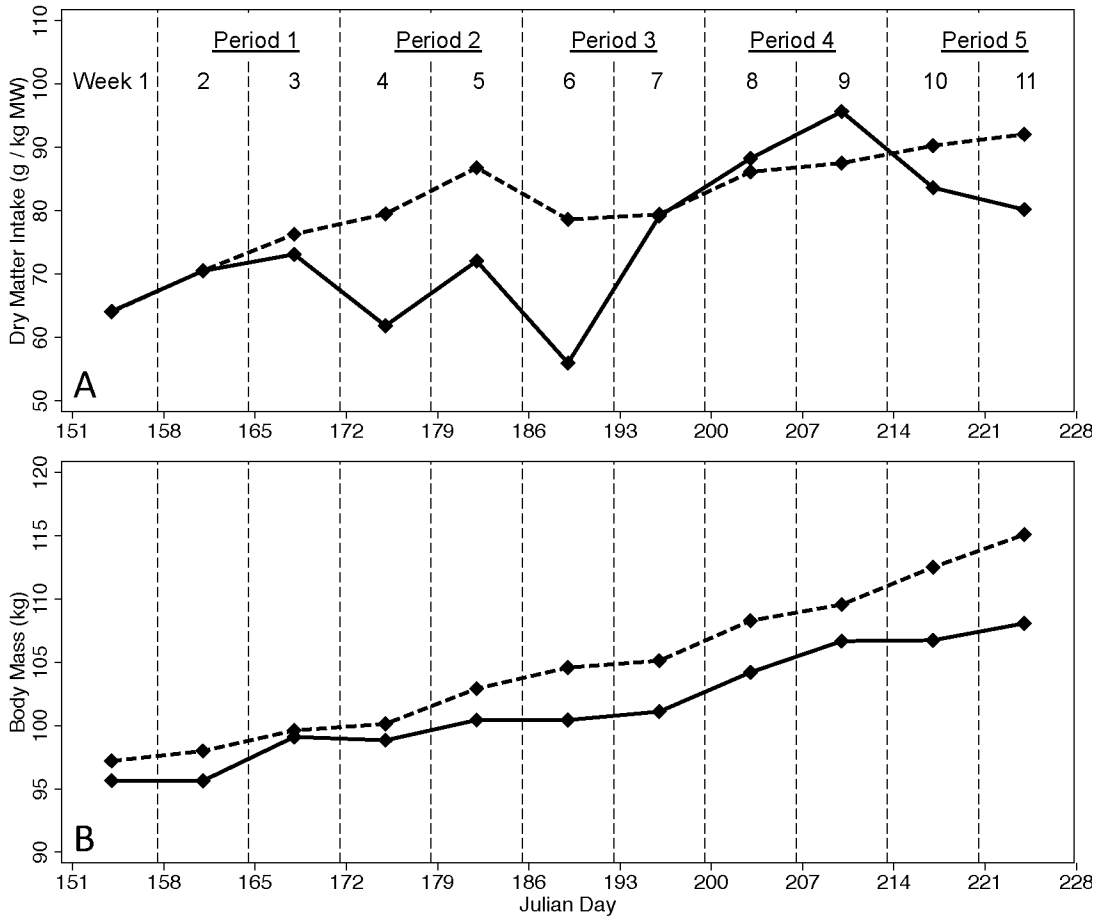

Figure 3.3. Average weekly dry matter intake of pelleted feed and average body mass for control (solid lines) and feeding trial (broken lines) caribou from 31 May to 15 August 2011 (Julian days 151 to 227) at the University of Alaska, Fairbanks – Robert G. White Large Animal Research Station, Fairbanks, Alaska, USA. (MW: metabolic weight = kg $^{0.75}$).

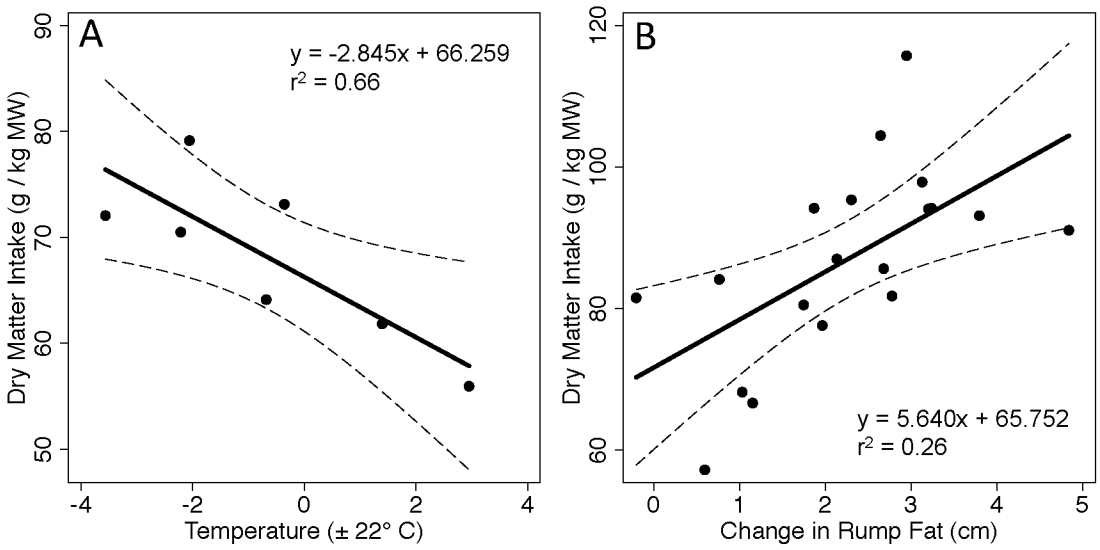

Figure 3.4. (A) The relationship between dry matter intake of pelleted feed and warm temperatures (with 95% confidence intervals) for control caribou in early summer. Temperature was calculated as the difference between maximum daily temperature and 22° C. Data were averaged for each week from 31 May to 18 July 2011 centered on the summer solstice. (B) The relationship between dry matter intake and change in rump fat (with 95% confidence intervals) for all caribou in late summer. Individual intakes were averaged over four weeks from 19 July to 15 August 2011 whereas changes in rump fat depth were from March to November 2011. (MW: metabolic weight = kg $^{0.75}$).

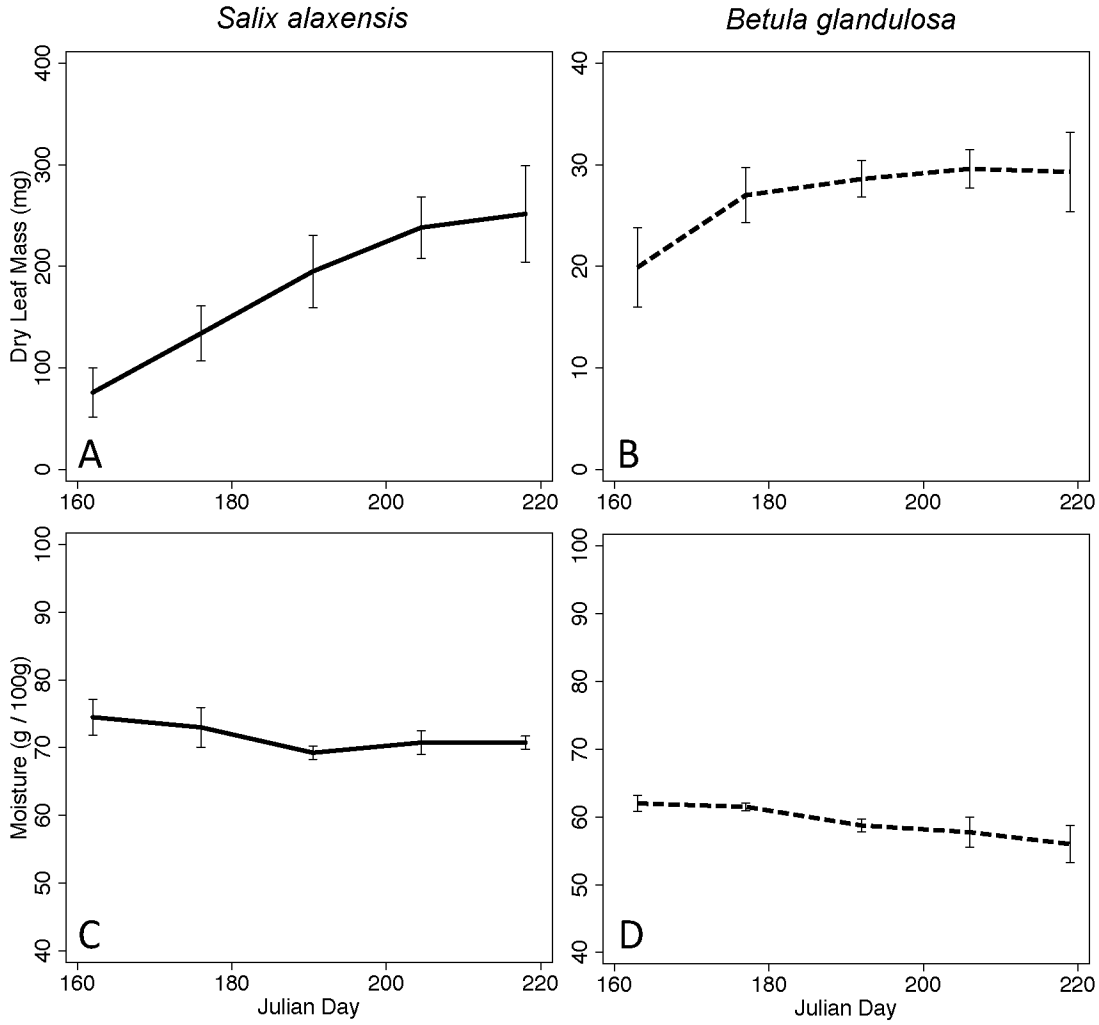

Figure 3.5. Dry mass of leaves (A and B) and moisture content of leaves and new woody growth (C and D) from feltleaf willow (*Salix alaxensis;* solid lines) and resin birch (*Betula glandulosa;* broken lines) that were selected by caribou during feeding trials from 6 June to 12 August 2011 (Julian days 157 to 224). All values are ± SD.

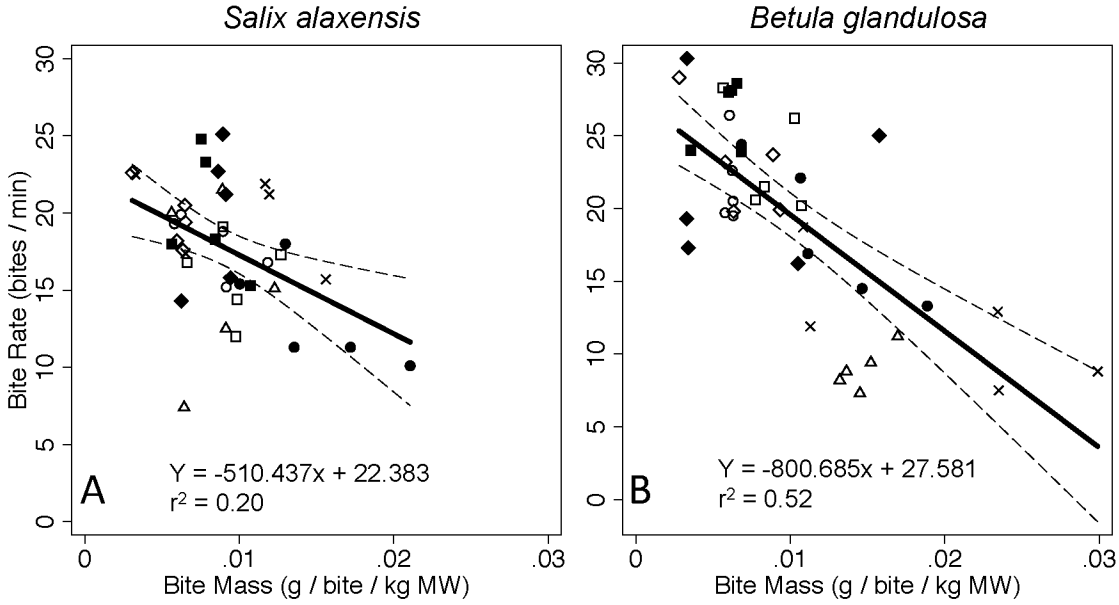

Figure 3.6. The relationship between bite rate and bite mass (with 95% confidence intervals) for (A) feltleaf willow (*Salix alaxensis*) and (B) resin birch (*Betula glandulosa*) that were selected by caribou during feeding trials from 6 June to 12 August 2011 (Julian days 157 to 224) at the University of Alaska, Fairbanks – Robert G. White Large Animal Research Station, Fairbanks, Alaska, USA. Each symbol represents a different animal (n = 8 per forage species). (MW: metabolic weight = $kg^{0.75}$).

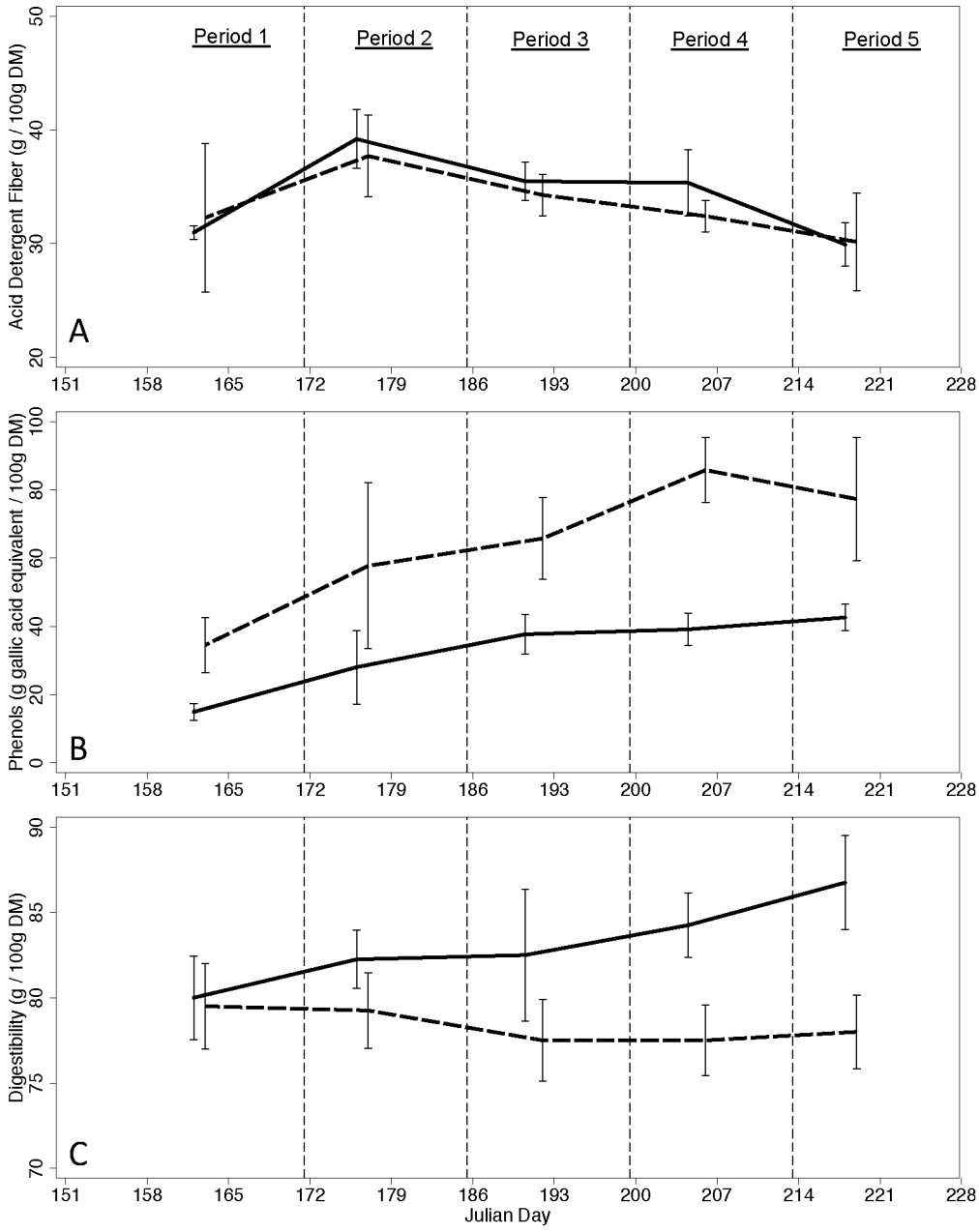

Figure 3.7. Concentrations of acid detergent fiber (A), total phenols (B), and digestibility (C) of leaves and new woody growth from resin birch (*Betula glandulosa*: broken lines) and feltleaf willow (*Salix alaxensis*: solid lines) that were selected by caribou in feeding trials from 6 June to 12 August 2011 (Julian days 157 to 224). All values are ± SD.

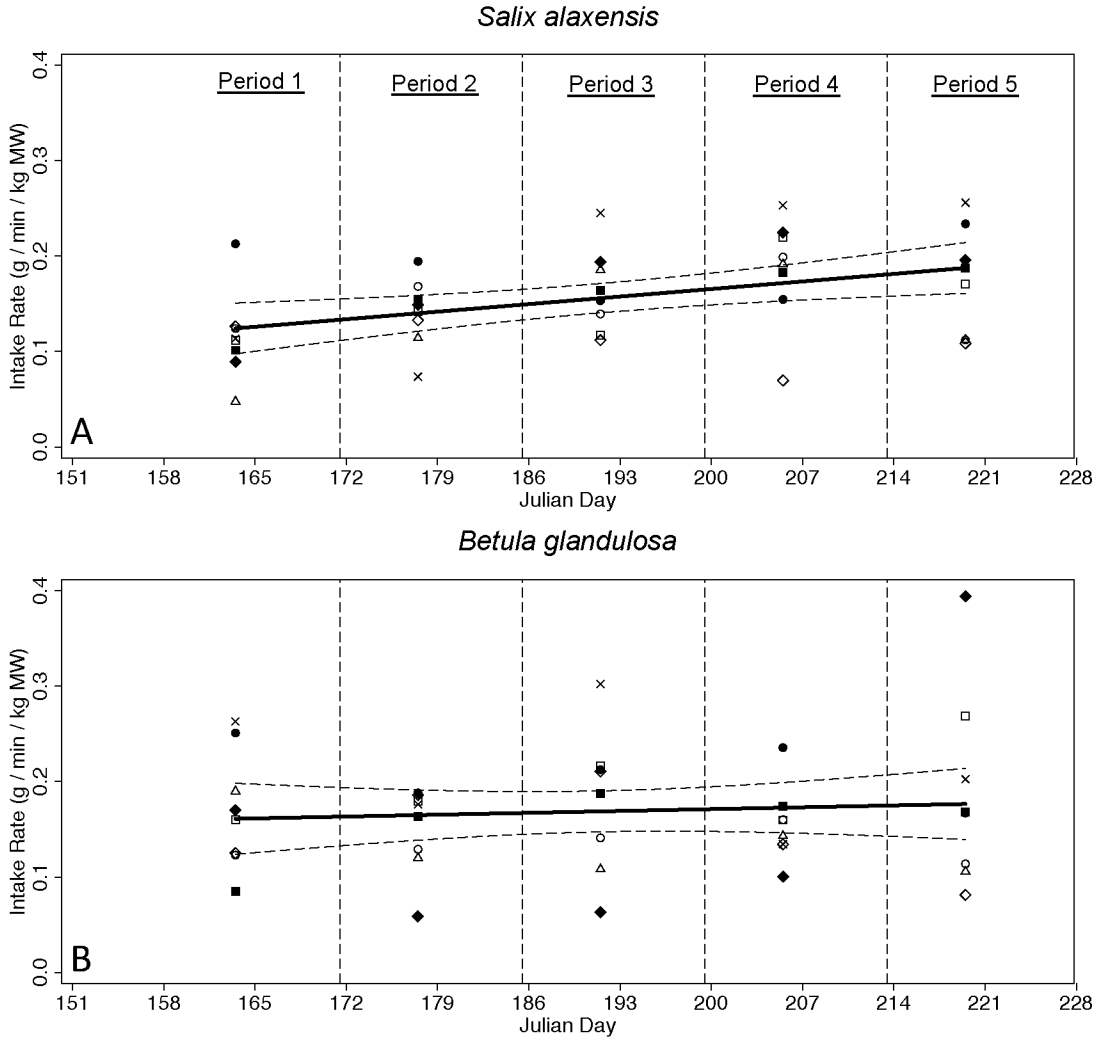

Figure 3.8. Instantaneous intake rate (with 95% confidence intervals) measured for caribou during feeding trials on (A) feltleaf willow (*Salix alaxensis*) and (B) resin birch (*Betula glandulosa*) from 6 June to 12 August 2011 (Julian Days 157 to 224) at the University of Alaska, Fairbanks – Robert G. White Large Animal Research Station, Fairbanks, Alaska, USA. Each symbol represents a different animal (n = 8 per forage species). (MW: metabolic weight = kg $^{0.75}$).

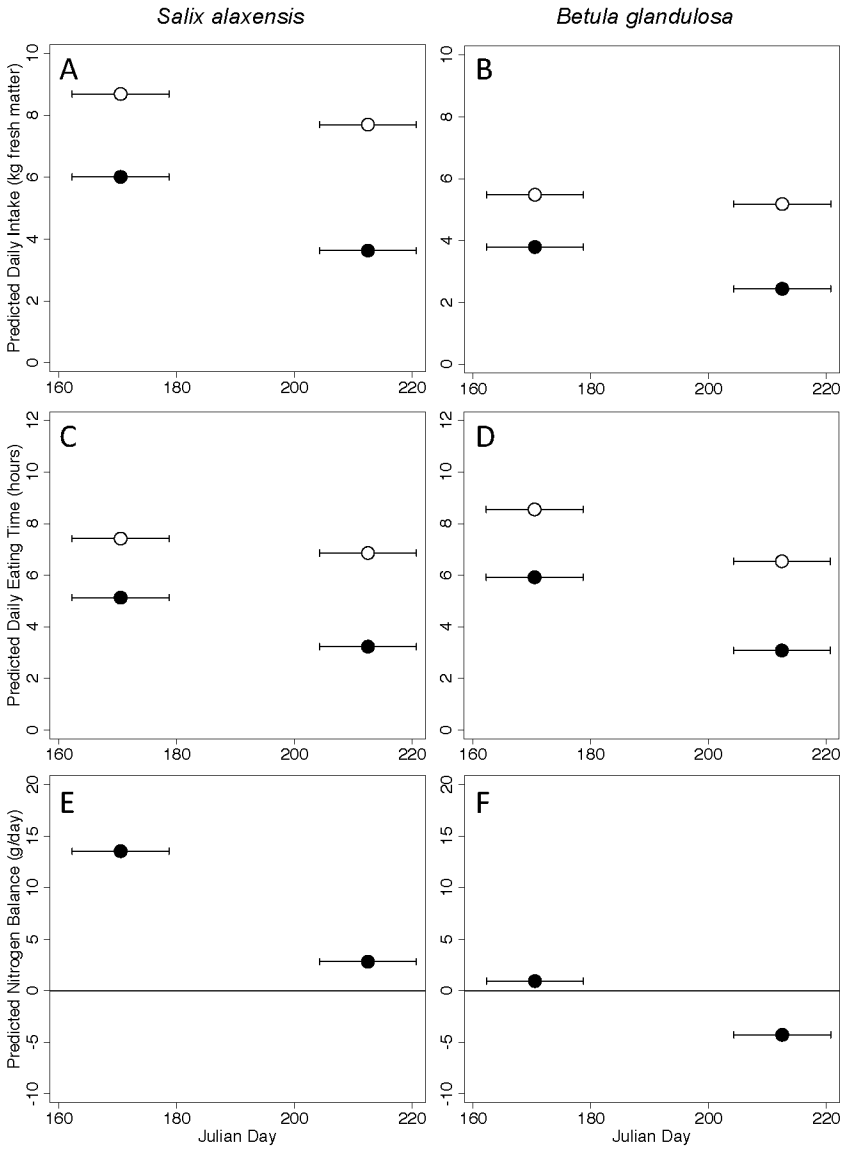

Figure 3.9. (A-B) Predicted daily intake of fresh mass and (C-D) predicted eating time to meet daily energy requirements for maintenance (black circles) and mass gain (white circles) for a 100-kg female caribou during early and late summer consuming resin birch (*Betula glandulosa*) or feltleaf willow (*Salix alaxensis*). (E-F) Predicted N balance for a 100-kg female caribou consuming feltleaf willow or resin birch to meet daily energy requirements for maintenance. (MW: metabolic weight = kg $^{0.75}$)

3.7 Tables

Table 3.1. Average composition of dietary dry matter for feltleaf willow (*Salix alaxensis*), resin birch (*Betula glandulosa*) and the pelleted ration consumed by caribou between 6 June and 12 August 2011.

Component	*Salix alaxensis*	*Betula glandulosa*	Pelleted ration
Ash (g/100g)[a,c]	7.9 ± 1.0	3.2 ± 0.4	7.0 ± 0.5
Organic Matter (g/100g)[a,c]	92.1 ± 1.0	96.8 ± 0.4	93.0 ± 0.5
Digestibility (g/100g)[a,b,c]	83.2[T] ± 3.3	78.4 ± 2.2	87 ± 0.4
Gross Energy (kJ/ 100g)[a,c]	19.0 ± 0.2	20.8 ± 0.1	18.0 ± 0.4
Neutral Detergent Fiber (NDF g/100g)[b,c]	48.6[T] ± 3.7	46.8 ± 5.8	36.8 ± 2.0
Acid Detergent Fiber (ADF g/100g)[b,c]	34.2[T] ± 3.9	33.4 ± 4.6	16.8 ± 1.0
Phenols (g gallic acid equivalent/ 100g)[a,b,c]	32.5[T] ± 11.7	64.2[T] ± 22.8	<1
Total Nitrogen (g/100g)[a,c]	2.7 ± 0.2	2.3[T] ± 0.3	2.7 ± 0.2
Nitrogen in ADF (g/100g)[a,b,c]	0.9 ± 0.3	1.3[T] ± 0.3	< 0.1
Available crude protein (g/100g)[a,b,c]	10.2 ± 1.9	6.2 ± 1.6	15.0 ± 0.8
Protein Precipitation Capacity (gBSA/100g)[a,b,c]	6.8 ± 2.3	15.9 ± 5.1	0
Digestible crude protein (g/ 100g)[a,c]	10.8 ± 1.4	7.2[T] ± 1.9	11.6 ± 1.3

[a] significant difference between feltleaf willow and resin birch $P < 0.05$
[b] significant difference between pelleted ration and feltleaf willow $P < 0.05$
[c] significant difference between pelleted ration and resin birch $P < 0.05$
[T] significant difference over the growing season $P < 0.05$

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3.9 Appendices

Appendix 3.1. Weekly average dry matter intake (g / kg body mass $^{0.75}$) of pelleted feed for control and trial caribou from 31 May to 15 August 2011, University of Alaska, Fairbanks - Robert G. White Large Animal Research Station, Alaska, USA.

	Animal ID							
Week	D01[C]	M05[C]	R02[C,1]	720[C]	D02[C]	H02[C]	D09[B]	H04[B]
1	76.9	96.4	60.6	40.0	56.2	54.5	73.7	73.7
2	66.6	100.0	75.4	40.1	78.7	62.2	96.5	77.5
3	81.4	108.9	88.8	50.8	48.9	59.9	83.3	61.8
4	90.3	77.5	85.1	38.3	44.8	35.1	88.2	93.1
5	86.3	49.6	99.7	42.8	85.1	68.8	86.4	75.5
6	57.5	69.9	79.7	42.5	32.6	53.3	93.2	97.9
7	110.5	102.5	93.6	40.5	60.8	66.9	75.6	88.2
8	112.1	113.7	89.3	45.2	87.4	81.8	85.0	110.2
9	107.1	120.2	18.4	58.7	102.0	90.3	82.6	92.4
10	73.8	104.1	41.4	61.5	98.0	80.8	98.4	97.0
11	49.5	79.8	51.7	63.3	85.1	69.1	98.3	77.1

[C] Control Animal; [B] Birch Trial Animal; [W] Willow Trial Animal; [1] Removed from study during the last 3 weeks due to illness

Appendix 3.1.

	Animal ID							
Week	R01[B]	W01[B]	D08[B]	M02[B]	M08[B]	R05[B]	D03[W]	M04[W]
1	67.3	70.7	74.7	62.0	62.3	66.9	56.0	73.0
2	86.0	93.8	73.9	61.8	56.2	68.4	63.0	74.4
3	99.3	91.4	86.0	78.1	73.4	85.5	69.7	82.1
4	101.7	114.3	62.6	68.6	65.6	73.0	83.7	75.6
5	88.1	101.3	82.3	86.1	60.3	97.0	77.3	99.2
6	99.6	115.2	71.2	70.0	66.2	65.5	69.9	87.5
7	85.1	99.6	82.4	86.3	81.3	84.9	59.1	67.0
8	72.6	118.7	77.5	78.5	76.4	79.4	86.6	77.4
9	85.7	101.6	79.2	62.9	107.9	97.1	80.2	71.7
10	126.1	133.2	75.6	63.0	85.0	69.0	82.2	106.9
11	107.1	109.4	78.0	68.2	107.0	90.9	77.0	92.0

[C] Control Animal; [B] Birch Trial Animal; [W] Willow Trial Animal

Appendix 3.1. continued

	Animal ID					
Week	W02[W]	W03[W]	718[W]	H03[W]	M06[W]	R03[W]
1	71.1	65.2	33.9	64.1	57.4	52.6
2	84.9	74.0	40.4	64.9	53.2	59.6
3	70.1	62.6	63.8	61.4	86.4	65.5
4	86.9	94.5	44.4	74.5	80.5	64.5
5	95.9	84.5	61.7	95.3	114.8	82.9
6	91.4	81.3	45.2	66.6	70.5	66.7
7	91.1	89.6	49.2	76.1	89.8	65.5
8	100.7	103.6	54.1	85.5	93.8	78.4
9	88.9	89.8	71.4	95.3	106.8	86.9
10	101.6	102.5	67.1	90.8	67.9	78.1
11	90.2	98.9	73.9	113.1	108.2	83.6

[C] Control Animal; [B] Birch Trial Animal; [W] Willow Trial Animal

Appendix 3.2. Weekly body mass (kg) of control and feeding trial caribou from 31 May to 15 August 2011 at the University of Alaska, Fairbanks - Robert G. White Large Animal Research Station, Alaska, USA.

	Animal ID							
Week	D01[C]	M05[C]	R02[C,1]	720[C]	D02[C]	H02[C]	D09[B]	H04[B]
1	82.2	93.3	111.9	78.2	92.7	115.6	93.6	89.1
2	81.0	93.6	109.6	79.0	92.8	117.8	96.2	88.8
3	84.4	102.2	112.6	80.0	97.8	117.6	100.4	85.8
4	86.4	101.6	114.2	81.0	96.8	113.0	99.8	90.2
5	88.8	100.4	119.0	81.2	99.6	113.6	100.6	90.2
6	90.6	98.8	118.2	82.6	97.2	115.2	102.2	94.0
7	92.6	98.0	117.2	84.4	99.2	115.2	101.8	95.4
8	93.8	102.0	121.4	87.2	99.6	121.2	104.6	99.6
9	96.2	109.2	117.2	90.2	105.0	122.2	105.8	102.6
10	95.4	112.0	108.6	91.0	106.8	126.6	107.2	103.2
11	100.3	113.4	106.4	94.5	110.4	123.4	112.8	107.0

[C] Control Animal; [B] Birch Trial Animal; [W] Willow Trial Animal; [1] Removed from study during the last 3 weeks due to illness

Appendix 3.2.

	Animal ID							
Week	R01[B]	W01[B]	D08[B]	M02[B]	M08[B]	R05[B]	D03[W]	M04[W]
1	85.8	112.9	75.5	117.8	107.2	98.6	99.8	90.2
2	84.8	111.0	79.0	116.2	107.8	100.0	100.4	90.8
3	87.4	116.2	80.4	117.6	110.6	101.8	102.0	93.8
4	87.8	118.4	80.8	118.8	110.4	102.0	104.4	92.8
5	90.6	121.8	82.2	123.2	110.8	106.2	108.2	95.2
6	91.4	124.8	82.2	124.6	110.8	109.2	107.6	101.2
7	95.0	127.2	85.0	124.4	113.0	108.4	104.8	96.2
8	94.0	131.4	85.6	130.8	116.2	112.4	108.6	99.0
9	93.8	134.2	84.0	128.2	117.8	114.4	109.2	99.6
10	100.0	137.8	90.0	132.2	123.0	117.4	109.2	101.8
11	100.4	143.0	91.0	128.9	125.5	118.4	112.2	108.1

[C] Control Animal; [B] Birch Trial Animal; [W] Willow Trial Animal

Appendix 3.2. continued

	Animal ID					
Week	W02[W]	W03[W]	718[W]	H03[W]	M06[W]	R03[W]
1	90.5	98.7	88.1	114.1	93.0	100.3
2	94.8	96.4	87.0	116.8	96.0	101.8
3	96.2	97.8	89.8	116.6	95.8	101.6
4	94.2	100.0	89.4	116.6	95.6	100.8
5	97.0	105.2	91.8	120.0	99.6	104.0
6	97.8	104.6	91.2	124.6	101.8	105.2
7	99.4	104.0	92.4	124.6	104.0	106.2
8	102.2	110.0	92.8	129.0	108.0	108.2
9	103.6	108.8	97.4	132.0	108.4	113.0
10	105.8	115.4	96.6	135.6	111.2	113.6
11	108.2	117.0	99.6	138.9	113.4	116.8

[C] Control Animal; [B] Birch Trial Animal; [W] Willow Trial Animal

Appendix 3.3. Akaike's Information Criterion (AIC) scores to select the most parsimonious model variables that described dry matter pelleted feed intake for control caribou from 31 May to 15 August 2011 at the University of Alaska, Fairbanks - Robert G. White Large Animal Research Station, Alaska, USA.

Entire 11 weeks		
Model Parameters	AIC Score	ΔAIC
Week Pen[1] Id[2]	543.61	
Week Pen[1] MKtemp[3] Id[2]	544.6	0.99
Week Pen[1] DL[4] Id[2]	544.76	1.15
Week Pen[1] Mktemp[3] DL[4] Id[2]	546.27	2.66
Week Id[2]	550.86	7.25
Week Mktemp[3] Id[2]	552.19	8.58
Week DL[4] Id[2]	552.37	8.76
Week Mktemp[3] DL[4] Id[2]	554.03	10.42

Weeks 1-7 (centered on solstice)		
Model Parameters	AIC Score	ΔAIC
Week Pen[1] MKtemp[3] Id[2]	347.46	
Week Pen[1] Mktemp[3] DL[4] Id[2]	349.45	1.99
Week Mktemp[3] Id[2]	352.45	4.99
Week Pen[1] Id[2]	353.21	5.75
Week Mktemp[3] DL[4] Id[2]	354.44	6.98
Week Pen[1] DL[4] Id[2]	355.01	7.55
Week Id[2]	357.09	9.63
Week DL[4] Id[2]	358.92	11.46

Weeks 8-11		
Model Parameters	AIC Score	ΔAIC
Week Pen[1] DL[4] Id[2]	182.64	
Week Pen[1] Mktemp[3] DL[4] Id[2]	184.62	1.98
Week Pen[1] Id[2]	184.71	2.07
Week Pen[1] MKtemp[3] Id[2]	185.03	2.39
Week DL[4] Id[2]	186.86	4.22
Week Id[2]	187.34	4.7
Week Mktemp[3] Id[2]	188.3	5.66
Week Mktemp[3] DL[4] Id[2]	188.84	6.2

[1] Holding pen
[2] Individual animal
[3] Maximum weekly temperature ± 22° C
[4] Day length (sunrise to sunset)

Appendix 3.4. Leaf mass and composition of dietary dry matter for feltleaf willow (*Salix alaxensis*) and resin birch (*Betula glandulosa*) used in feeding trials for caribou from 6 June to 12 August 2011 (JD - Julian days 157-224) at the University of Alaska, Fairbanks -Robert G. White Large Animal Research Station, Alaska, USA.

	Salix alaxensis									
JD	Leaf Mass	Ash	Moist[1]	NDF[2]	ADF[3]	Digest[4]	Total N[5]	ADF N[6]	Phenol[7]	PPC[8]
	mg	g / 100g	g / 100g	g / 100g	g/ 100g	g / 100g	g / 100g	g / 100g	g / 100g	g / 100g
157	51.8	7.7	73.2	46.4	31.2	82.8	2.4	1.3	13.3	6.7
160	59.0	8.7	78.2	46.6	31.7	78.2	2.8	0.7	16.4	7.1
164	92.6	6.7	75.2	44.9	30.3	80.5	3.2	0.7	17.6	4.8
167	100.3	8.1	72.1	45.3	30.8	78.4	2.5	0.8	12.5	5.7
171	105.0	6.7	76.0	48.0	38.6	82.4	3.0	1.4	19.7	9.3
174	135.8	7.4	70.8	54.9	42.7	84.5	2.4	0.9	17.9	11.3
178	169.7	6.5	69.7	51.3	36.5	80.4	2.4	0.6	38.8	9.1
181	125.6	7.5	74.7	52.2	39.0	82.6	2.6	0.6	35.8	5.5
186	161.3	6.6	70.4	54.9	37.2	76.8	2.7	0.8	40.2	5.6
189	175.2	7.3	68.6	48.8	33.2	83.4	2.7	0.9	33.3	6.3
192	201.7	7.2	70.4	52.4	36.2	83.6	2.8	1.2	32.6	4.9
195	242.3	8.5	68.4	50.0	35.3	86.4	2.7	1.0	44.7	3.0
199	205.2	8.2	73.3	43.8	37.7	83.1	2.8	1.4	35.8	9.5
202	220.0	9.3	69.3	48.5	32.7	86.6	2.6	1.0	42.0	2.2
207	262.2	10.6	70.9	48.9	38.0	82.6	2.9	1.1	34.5	7.9
210	265.4	7.4	70.1	54.0	33.0	83.6	2.6	0.8	44.2	8.3
213	228.7	8.1	69.8	42.3	32.5	84.2	2.3	1.0	41.9	9.4
216	240.0	8.6	69.7	45.7	28.0	88.0	2.5	0.7	46.6	5.3
220	321.2	7.5	71.3	45.1	29.0	90.4	2.7	0.8	37.6	7.7
223	216.4	8.9	72.2	47.9	30.3	84.7	2.7	1.0	44.4	5.5

[1] Moisture; [2] Neutral Detergent Fiber; [3] Acid Detergent Fiber; [4] Digestibility; [5] Total Nitrogen; [6] ADF Bound Nitrogen; [7] Total Phenols (g Gallic Acid Equivalent/ 100g); 8 Protein Precipitation Capacity (g Bovine Serum Albumin / 100g)

Appendix 3.4. continued

JD	*Betula glandulosa*									
	Leaf Mass	Ash	Moist[1]	NDF[2]	ADF[3]	Digest[4]	Total N[5]	ADF N[6]	Phenol[7]	PPC[8]
	mg	g / 100g	g / 100g	g / 100g	g/ 100g	g / 100g	g / 100g	g / 100g	g / 100g	g / 100g
158	16.8	2.8	61.3	49.8	32.8	82.8	2.9	1.6	31.1	
161	16.4	2.9	63.1	47.4	38.1	78.2	2.6	1.7	45.0	17.0
165	23.2	3.0	60.7	57.4	35.2	80.5	2.6	1.7	25.9	11.3
168	23.3	3.0	62.6	43.2	23.0	78.4	2.7	0.9	36.1	18.3
172	24.5	2.7	61.5	56.5	40.8	82.4	2.6	1.6	43.5	19.2
175	24.9	3.4	61.5	54.6	40.7	84.5	2.4	1.7	38.7	10.3
179	30.1	4.4	61.6	38.5	35.4	80.4	2.1	1.3	56.3	23.8
182	28.5	3.2	61.4	46.8	33.9	82.6	2.3	1.3	92.5	14.6
187	28.4	2.6	58.8	41.3	35.2	76.8	2.0	1.2	74.9	21.0
190	27.0	3.1	60.2	45.8	36.3	83.4	2.2	1.3	69.5	9.1
193	27.7	2.9	57.7	47.0	33.1	83.6	1.9	1.2	48.1	17.5
196	31.1	3.0	58.3	44.7	32.4	86.4	2.1	1.2	70.6	16.2
200	31.5	3.1	56.9	37.0	30.5	83.1	2.1	1.1	93.4	19.6
203	30.3	3.7	59.6	39.8	32.8	86.6	2.3	1.3	93.8	22.2
208	27.1	3.0	58.5	43.8	32.6	82.6	1.9	1.1	81.8	11.0
211	29.5	3.4	54.7	48.6	33.8	83.6	2.1	1.2	74.2	6.3
214	29.2	3.2	54.1	45.3	29.4	84.2	1.9	1.0	69.0	20.2
217	33.7	3.2	55.1	45.5	24.8	88.0	1.7	0.7	104.3	21.7
221	24.2	3.9	60.0	56.1	35.2	90.4	2.2	1.2	65.9	11.0
224	30.2	3.8	55.2	47.8	31.2	84.7	2.2	1.0	70.0	13.1

[1] Moisture; [2] Neutral Detergent Fiber; [3] Acid Detergent Fiber; [4] Digestibility; [5] Total Nitrogen; [6] ADF Bound Nitrogen; [7] Total Phenols (g Gallic Acid Equivalent/ 100g); 8 Protein Precipitation Capacity (g Bovine Serum Albumin / 100g)

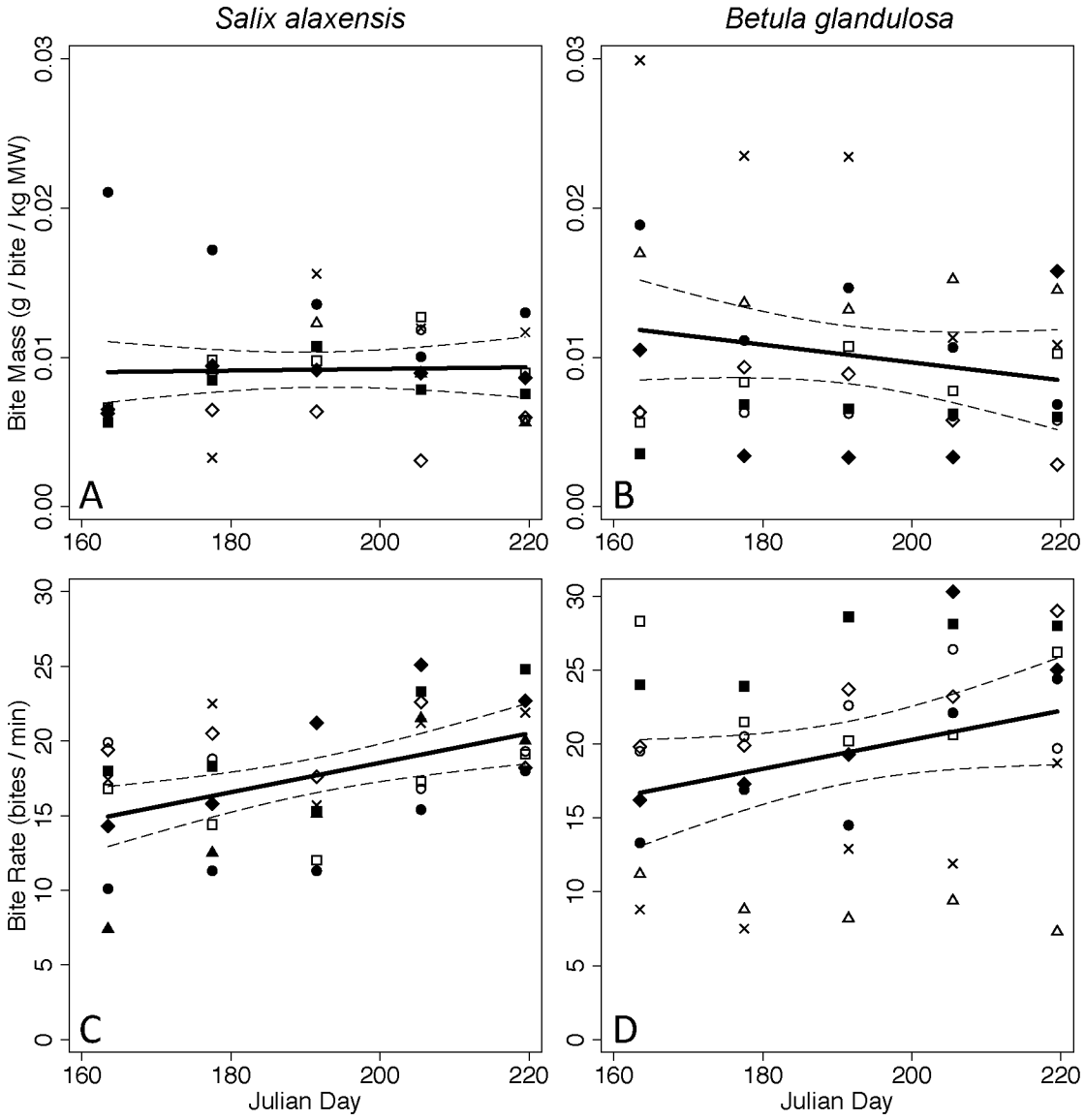
Appendix 3.5. Individual bite mass (g / bite), bite rate (bites / minute), and intake rate (g / minute) for caribou documented during feeding trials on feltleaf willow (*Salix alaxensis*) and resin birch (*Betula glandulosa*) during each two-week period from 6 June to 12 August 2011 at the University of Alaska, Fairbanks - Robert G. White Large Animal Research Station, Alaska, USA.

Salix alaxensis				
Id	Period	Bite Mass	Bite Rate	Intake Rate
718	1	0.60	10.1	6.1
	2	0.51	11.3	5.8
	3	0.42	11.3	4.7
	4	0.30	15.4	4.6
	5	0.36	18.0	6.4
D03	1	0.18	19.9	3.6
	2	0.30	18.8	5.7
	3	0.32	15.2	4.8
	4	0.36	16.8	6.1
	5	0.19	19.3	3.7
H03	1	0.24	18.0	4.3
	2	0.32	18.3	5.9
	3	0.40	15.3	6.2
	4	0.26	23.3	6.1
	5	0.26	24.8	6.6
M04	1	0.22	16.8	3.6
	2	0.31	14.4	4.5
	3	0.29	12.0	3.4
	4	0.37	17.3	6.4
	5	0.33	19.1	6.3
M06	1	0.24	17.4	4.2
	2	0.12	22.5	2.8
	3	0.48	15.7	7.6
	4	0.35	21.2	7.4
	5	0.44	21.9	9.6
R03	1	0.18	14.3	2.6
	2	0.27	15.8	4.2
	3	0.34	21.2	7.3
	4	0.32	25.1	8.1
	5	0.25	22.7	5.7
W02	1	0.18	19.4	3.5
	2	0.16	20.5	3.2
	3	0.21	17.6	3.7
	4	0.15	22.6	3.3
	5	0.20	18.2	3.6
W03	1	0.23	7.4	1.7
	2	0.28	12.5	3.5
	3	0.43	15.1	6.4
	4	0.34	21.5	7.3
	5	0.20	20.0	3.9

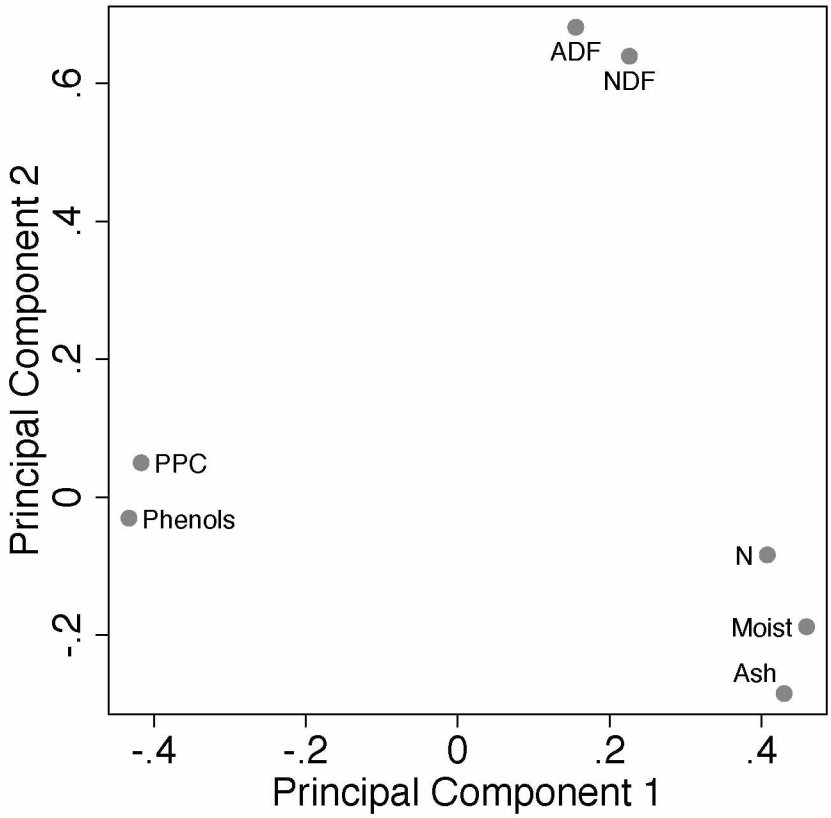
Appendix 3.5. continued

Betula glandulosa				
Animal Id	Period	Bite Mass	Bite Rate	Intake Rate
D08	1	0.46	13.3	6.2
	2	0.29	16.9	4.9
	3	0.41	14.5	6.0
	4	0.32	22.1	7.0
	5	0.21	24.4	5.0
D09	1	0.24	19.5	4.8
	2	0.16	20.5	3.4
	3	0.18	22.6	4.0
	4	0.17	26.4	4.6
	5	0.16	19.7	3.2
H04	1	0.11	24.0	2.7
	2	0.16	23.9	3.8
	3	0.17	28.6	4.9
	4	0.17	28.1	4.9
	5	0.24	28.0	6.6
M02	1	0.22	28.3	6.2
	2	0.29	21.5	6.2
	3	0.39	20.2	7.9
	4	0.32	20.6	6.5
	5	0.36	26.2	9.4
M08	1	1.02	8.8	8.9
	2	0.79	7.5	5.9
	3	0.78	12.9	10.1
	4	0.43	11.9	5.1
	5	0.44	18.7	8.3
R01	1	0.29	16.2	4.7
	2	0.10	17.3	1.7
	3	0.15	19.3	2.8
	4	0.13	30.3	3.8
	5	0.47	25.0	11.8
R05	1	0.22	19.8	4.3
	2	0.25	19.9	5.0
	3	0.32	23.7	7.7
	4	0.16	23.2	3.6
	5	0.08	29.0	2.4
W01	1	0.65	11.2	7.3
	2	0.48	8.8	4.2
	3	0.47	8.2	3.9
	4	0.61	9.4	5.8
	5	0.63	7.3	4.6

Appendix 3.6. Bite mass (A, B; with 95% confidence intervals) and bite rate (C, D; with 95% confidence intervals) measured for caribou during feeding trials on feltleaf willow (*Salix alaxensis*) and resin birch (*Betula glandulosa*) from 6 June to 12 August 2011 (Julian Days 157 to 224) at the University of Alaska, Fairbanks - Robert G. White Large Animal Research Station, Alaska, USA. Each symbol represents a different animal (n = 16). (MW: metabolic weight = kg $^{0.75}$).



Appendix 3.7. Principal component loading plot for plant characteristics of feltleaf willow (*Salix alaxensis*) and resin birch (*Betula glandulosa*) used in feeding trials for caribou from 6 June to 12 August 2011 (Julian days 157-224) at the University of Alaska, Fairbanks -Robert G. White Large Animal Research Station, Alaska, USA. (NDF – Neutral Detergent Fiber; ADF – Acid Detergent Fiber; PPC – Protein Precipitation Capacity; Moist – Moisture; N – Total Nitrogen).



Chapter 4: Conclusion

4.1 Overview

Caribou and reindeer provide food and income for northern societies (Klein 1991) around the world. Given their importance, understanding how natural and anthropogenic disturbances affect *Rangifer* has resulted in an abundance of research on caribou and reindeer, often with international implications. My research attempted to improve our understanding of how *Rangifer* can meet their daily energy requirements while adapting to changing conditions in their environment. The objectives for this thesis were: 1) to evaluate how caribou and reindeer tolerate short-term food restrictions in late winter and early spring, similar to lost foraging time associated with an icing event or deep snow; and 2) to evaluate how caribou respond to changing quality of two species of browse (resin birch - *Betula glandulosa*; feltleaf willow - *Salix alaxensis*) over the growing season, as shrubs have been expanding into tundra habitats used by caribou. To complete my research, I successfully built 30 Calan gate feeder systems, and trained 24 caribou and 5 reindeer to open their individual gate and access their daily food, while maintaining them in a herd setting.

4.2 Food Shortages in Late Winter

To determine the affects of short-term food restrictions on caribou and reindeer, I measured individual food intake of 21 caribou and 5 reindeer using the Calan gate feeders. I collected body mass measurements on each animal at least twice a week, and before and after each restriction event. I gathered daily activity counts on a subset of caribou and reindeer to evaluate if restrictions affected their daily activity. Maximum

rump fat was measured with an ultrasound before the study began to see if caribou with high energy reserves from rump had a different response in food intake, body mass, or activity to food shortages compared to leaner caribou.

4.2.1 Food Intake in Late Winter

During late winter, when caribou have reduced intakes (Parker et al. 2005, Barboza and Parker 2008), I found that caribou can increase daily food intake the day following restriction to compensate for a loss in foraging time. This indicates that caribou do not eat at maximum levels of intake on a daily basis, and implies that caribou have "spare capacity" to accommodate, digest and metabolize extra food (Baker and Hobbs 1987, McWilliams and Karasov 2005, Barboza and Hume 2006, Clauss et al. 2007). This "spare capacity" gives caribou the flexibility to loose up to 2.25 days of weekly food intake if they have sufficient forage (both quality and quantity) and time (minimal disturbances) in the days following restriction to compensate for food shortages. Furthermore, if caribou can maintain the maximum daily intakes that I observed after restrictions, caribou could utilize lower quality forage and obtain the same digestible energy intakes that I observed on control animals eating high quality pelleted feed. As caribou move across the landscape in late winter and early spring, they may encounter patches of high quality vegetation associated with variations in snowmelt and terrain. In these vegetation patches, caribou could increase their daily intakes with "spare capacity" to take advantage of this high quality vegetation.

4.2.2 Body Mass in Late Winter

Although body mass declined during the winter study for all caribou, I did not find a difference in weekly body mass change between restricted and control caribou. Restricted caribou lost an average of 3% body mass the day following food restriction, but regained 1-2% body mass on the days after restriction when they had *ad libitum* food. The overall decline in body mass was probably associated with loss of fat stores similar to those observed in caribou in late winter when photoperiod is increasing (Mautz 1978, Adamczewski et al. 1987, Barboza and Parker 2008). I found a positive relationship between body mass and initial rump fat for caribou, which was similar to that described for wild caribou (Gerhart et al. 1996). Furthermore, I also found that caribou that had larger fat stores at the beginning of this study lost more weight over the 5 weeks than leaner animals. This indicates that larger caribou, with larger fat stores, subsequently lost more mass than smaller caribou with smaller fat stores over the study. This would imply that those animals in the middle of winter with high rump fat utilize this energy, and draw down body fat reserves to a set point at the end of winter to a similar level of body fat as the leaner animals, which has been observed in moose in Alaska (Kraft 2011). This loss of body fat at the end of winter may be a way that caribou lower their chances of heat stress during the long, warm days around the summer solstice when I observed a suppression of food intake.

4.2.3 Activity in Late Winter

Control and restricted caribou synchronized their daily activity in both restricted and unrestricted weeks, exhibiting similar levels of activity to wild *Rangifer* (Collins and

Smith 1989, Maier and White 1998, Colman et al. 2004). I did observe a small affect of body fat on activity levels, that is, caribou with lower fat reserves had slightly higher activity levels than caribou with larger fat reserves. This slight difference is probably associated with smaller animals spending more time feeding, while larger animals still maintained a similar activity pattern by synchronizing with the herd. I also found that at the end of the study, activity levels of caribou increased with corresponding increases in temperature and photoperiod. This increase in caribou activity may be tied to an endogenous cue associated with migratory behaviors observed in captive and wild herds of caribou (Maier and White 1998).

4.2.4 Caribou vs. Reindeer in Late Winter

I found that reindeer and caribou with similar body condition also had similar daily dry matter intakes at the beginning of the winter study; however, daily dry matter intakes for reindeer declined and were lower than those of caribou by the end of the study. Furthermore, I observed that as both photoperiod and ambient air temperature increased, daily dry matter intakes declined for reindeer in non-restriction weeks. Reindeer also were able to increase digestive efficiency over the study, but could not offset a decline in digestible intake, whereas digestive efficiency of caribou remained constant. Reindeer lost body mass over the 5-week trial. Mass changes were similar to caribou, that is, 1-3% body mass was lost on the days following restriction but regained in the days after restriction. I also found that reindeer had lower activity than caribou in similar body condition over the entire study, and were not influenced by photoperiod or ambient air temperature as observed in wild reindeer (Colman et al. 2004). Caribou may inherently

have higher activity levels, as wild caribou are more migratory in nature, compared to most domestic reindeer that are more sedentary in nature. Also, at the beginning of this study, other reindeer on the facility were calving, and by the end of the study, other caribou on the facility were calving as well and may have influenced either caribou or reindeer in this study. To minimize this discrepancy, future studies comparing caribou and reindeer should be completed before or after calving, or encompass enough time on either side of parturition for both subspecies to determine any influences from other females on the facility.

4.3 Forage Quality in Summer

To evaluate how caribou are influenced by shrub quality over the growing season, I conducted over 160 hours of individual caribou feeding trials with feltleaf willow and resin birch. I analyzed nutrients, anti-nutrients, digestibility and average leaf size of both forages to determine if instantaneous intake rate was influenced by vegetative characteristics. I also measured daily food intake and weekly body mass of 22 caribou for 11 weeks over the growing season to determined background intake requirements and mass gain. I used the data gathered from feeding trials, daily pelleted feed intakes, and mass gain to estimate if caribou could meet daily energy demands for maintenance and mass gain on diets consisting entirely of feltleaf willow or resin birch. Shrubs are already a significant component of the summer diet of caribou; however, as shrubs expand into tundra they may displace forbs and graminoids that are often high quality foods.

4.3.1 Summer Intake and Mass Gain

Similar to other studies, I observed that intake of pelleted rations and body mass of caribou increased over the summer (Larsen et al. 1985, Tyler et al. 1999). I found that caribou that gained the most fat over the summer had higher intakes in late summer, a time when body mass gain is mainly associated with accumulation of fat stores (Chan-McLeod et al. 1994). I also found that during the long days in the weeks before and after the summer solstice, high temperatures negatively affected caribou food intake, similar to lower activity levels observed in wild caribou at warmer temperatures (Mörschel and Klein 1997). By suppressing food during long, warm days, caribou would also decrease diet-induced thermogenesis and minimize heat stress (Barboza et al. 2009). Furthermore, if caribou wait until the end of summer to accumulate fat stores, it may allow caribou to avoid heat stress during the warm part of the growing season.

4.3.2 Summer Forage Attributes

Over the course of the growing season, I observed that caribou selected a range of plant material from both feltleaf willow and resin birch, progressing from new woody growth and leaf clusters in the early part of the season, to predominantly leaves at the end of summer. Furthermore, individual caribou consuming resin birch predominately stripped leaves, whereas those consuming feltleaf willow predominately selected individual leaves to achieve the same bite mass. However, I did observe different caribou stripping and selecting individual leaves on both species of browse over the entire growing season. Caribou may inherently select forage along a fiber gradient associated with tensile strength of the forage (Searle and Shipley 2008), that is, as fiber increases in new woody

growth, increases in tensile strength reduce the likelihood of cropping this material. This allowed caribou to select plant parts from each forage that was at least 75% digestible during short-term feeding bouts over the entire growing season.

4.3.3 Summer Instantaneous Intake Rates

I found no difference in bite mass for caribou when foraging on resin birch or feltleaf willow over the growing season. Bite rates on both forages increased over the summer and probably were associated with increased background intake of pelleted feed. I did observe that caribou had slightly higher bite rates on resin birch than feltleaf willow; however, large individual variation in bite rate on resin birch facilitated this difference. As expected, bite rate decreased with increasing bite mass, but this relationship was predominately influenced by individual variations in bite rate and bite mass. Individuals with large bite sizes had lower bite rates, whereas individuals with smaller bite sizes had higher bite rates. I documented bite rates that were similar to those observed for direct observation of woodland caribou (Shipley and Spalinger 1992, Rominger et al. 2000). During feeding trials I did observe that caribou take several false bites where they did not crop any vegetation, thus my estimates of bite rate were considerably lower than bite rates obtained through distance observation or devices measuring jaw movement that may not have distinguished these false bites (Trudell and White 1981, Kuropat 1984). Finally, I found that instantaneous intake rates of both forages were not different, and had little, if any change over the summer. This implies that on these short-term feeding trials, plant characteristics, such as phenols that increased over the season, did not influence intake rates.

4.3.4 Summer Forage Requirements

I estimated daily intake of fresh resin birch or feltleaf willow to meet energy requirements for a 100-kg female caribou by using the energy requirements estimated from the pelleted ration. I found that caribou can consume enough resin birch or feltleaf willow to meet daily energy requirements for maintenance and mass gain, and that caribou would have enough time in each day to consume either forage to meet energy requirements. However, my data indicate that caribou could be in negative nitrogen balance, particularly for a diet of resin birch (McEwan and Whitehead 1970). Furthermore, by consuming a diet comprised exclusively of feltleaf willow or resin birch, caribou would ingest plant secondary metabolites. For resin birch, total phenols ingested at the end of the summer to meet energy requirements for mass gain would be 4 times higher than total phenols ingested from feltleaf willow to meet maintenance requirements at the beginning of summer. Although short-term, instantaneous intake rates of each forage was not influenced by plant characteristics such as phenols, it is possible that post ingestive cues from plant secondary metabolites in either shrub may negatively influence intakes the following day.

4.4 Grand Finale

My study indicates that caribou and reindeer can tolerate disturbances that affect forage quantity and quality if they have alternative forage or can quickly move to other forage patches. In late winter, *Rangifer* that encounter short-term food shortages can compensate if adequate food of equal quality is available in a few days following the restriction. Along migration routes in late winter or early spring, the ability for caribou to

have "spare capacity" may allow them to consume lower quality food by increasing daily intake, or quickly consuming large amounts of high-quality forage encountered on the landscape or at stopover sites (Sawyer and Kauffman 2011). In summer foraging patches that are increasing in shrub density, caribou may need adequate alternative sources of forage. Caribou would have to consume the alternative forage at the same intake rate as resin birch or feltleaf willow (e.g., caribou may achieve lower intake rates on high-quality forbs that are spread out in a patch than on a single shrub). These alternative forages would need to have a higher available crude protein content to supplement a low-nitrogen, shrub-dominated summer diet. Given that the caribou in this study were maintained on a balanced pelleted diet, the direct affects of plant secondary metabolites may have been dampened. It is also possible that caribou can tolerate these high-phenol contents as reindeer have been found to degrade the phenolic secondary compound usnic acid from lichens (Sundset et al. 2010); however, a direct food intake study feeding caribou a diet of a chemically defended shrub, such as resin birch, would be required to confirm this tolerance. From a nutritional standpoint, understanding how caribou can subsist on these shrubs will become an increasingly important metric in managing wild caribou herds as the arctic and boreal regions continue to change.

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